

A Revision of the North American Species of Drepanocladus

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STUDIES IN DREPANOCLADUS—I.¹

History, Morphology, Phylogeny, and Variation

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HISTORICAL ACCOUNT OF THE GENUS

Although the name *Drepanocladus* was not proposed until 1851, several of the species included were described under *Hypnum* by Hedwig and previous workers. It is therefore necessary to trace the concept of the genus *Drepanocladus* from the beginning of bryological nomenclature.

In his fundamental work, *Species Muscorum*, Hedwig (1801), included only three of the species now placed in *Drepanocladus*—*Hypnum aduncum*, *H. fluitans* and *H. uncinatum*. Turner (1804) in his *Spicilegium* considered these three and added *Hypnum revolvens*. Bridel (1812), in the second supplement of *Muscologia Recentiorum*, added *Hypnum lycopodioides*.

As early as 1827 the species of *Hypnum* with unicostate, falcate-secund leaves were recognized as a unit and, in this *Bryologia Universa*, Bridel (1827) segregated them under the heading, which may be interpreted as a section, "Adunci." In this work he placed 65 of the species of *Hypnum* in the subgenus *Stereodon*; 8 of these are included under "Adunci." He does not state that *Stereodon* is a subgenus but it is not numbered in the series with the genera so cannot be considered a genus. That he was familiar with the concept of the subgenus is evidenced by the statement in the preface: "Sic genus *Campylopus* melius instituimus, speciebus omnibus quae calyptra mitriformi utuntur ab illo detractis et in genus novum nobis *Dryptodon* dictum quodque *Grimmiam* tanquam subgenus continuat, conflatis." The species included under "Adunci" are *Hypnum Stereodon aduncus*, *fluitans*, *uncinatus*, *lycopodioides*, and *scorpioides* with three other species still in *Hypnum* and one species now in *Hylocomium*.

In his *Synopsis Muscorum*, Müller (1851) further segregated these species into section *Mallacodium* and created the name *Drepanocladus* for the subsection which included *H. riparium* (now in *Leptodictyum*), *H. uncinatum*, *H. fluitans*, *H. aduncum*, *H. revolvens*, and *H. paradoxum*.

The first monographic treatment of the present species of *Drepanocladus* appeared in the *Bryologia Europaea* (1854, 1866) where the group was treated as Section VII of *Hypnum* under the descriptive heading: "Caulis erectus vel prostratus, folia falcato-secunda, unicostata." To the species earlier considered were added *H. exannulatum* in the monograph and *H.*

¹ This is the first of a series of four articles on *Drepanocladus*; the others will appear in BRITTONIA, THE AMERICAN MIDLAND NATURALIST, and THE BRYOLOGIST.

Cossoni, *H. Sendtneri*, and *H. vernicosum* (described first in 1861 by Lindberg) in the first supplement. Our present species *Drepanocladus Kneiffii* appeared first in the *Bryologia Europaea* under the genus *Amblystegium*. All the species are described with the completeness and accuracy and illustrated with the beauty characteristic of the *Bryologia Europaea*.

Bridel's recognition of the group "Adunci" was followed by subsequent workers in *Hypnum*. In *The Musci and Hepaticae of the United States* Sullivant (1856) proposed the subgenus *Harpidium* to include essentially the same species, namely, *Hypnum aduncum*, *H. uncinatum*, *H. revolvens*, and *H. fluitans*. Schimper, in his two editions of *Synopsis Muscorum Europaeorum* (1860, 1876) placed in the subgenus *Harpidium* *Hypnum Kneiffii*, *H. aduncum*, *H. lycopodioides*, *H. exannulatum*, *H. fluitans*, *H. revolvens*, *H. uncinatum* (in ed. 1), and *H. vernicosum*, *H. Cossoni*, *H. Sendtneri*, *H. hamifolium*, *H. pseudostramineum*, and *H. Molendoanum* (in ed. 2).

De Notaris (1838) in his *Syllabus Muscorum* included *H. scorpioides*, *H. lycopodioides*, *H. aduncum*, *H. fluitans*, and *H. uncinatum* with several other species of *Hypnum* in Section "Adunca" of *Hypnum*. However in his *Bryologia Italiana* (1869) he transferred the following species to *Amblystegium* II *Macrophylla* (which included also several present species of *Amblystegium* and *Hypnum*): *H. Rotae*, *H. lycopodioides*, *H. Sendtneri*, *H. revolvens*, *H. fluitans*, *H. uncinatum*, *H. exannulatum*, and *H. Kneiffii*.

Hartman and Lindberg, in Hartman's *Skandinaviens Flora* (ed. 5, 1849; ed 8, 1861; and ed. 9, 1864) proposed the new species *Hypnum badium*, *H. vernicosum*, and *H. intermedium* but did not add, in their floristic treatments, anything new to the concept of the group as a whole.

By 1869 the concept of the genus *Drepanocladus* as we know it today was well defined and most of our present species had been described. The process until this time had been to describe the species and to group them according to their relationships. Beginning in 1880 with Sanio's work a tendency developed to split this small group of species into many species, subspecies, varieties, and forms. The present genus *Drepanocladus* was shifted from *Amblystegium* to *Hypnum* and back again several times during this period.

Carl Sanio, in numerous papers from 1880-1887, treated the group as the subgenus *Harpidium* of *Hypnum*.² His classification, following a

² Commentatio de *Harpidiis* europaeis inductiva. Bot. Centralbl. 1880 (Beilage 2): 1-24. 1880. Additamentum in *Hypni adunci* cognitionem. Bot. Centralbl. 5(3): 93-95. 1881. Additamentum secundum in *Harpidiarum* cognitionem. Bot. Centralbl. 13(13): 425-440. 1883. Beschreibung der Harpidien, welche vornehmlich von Dr. Arnell während der Schwedischen Expedition nach Sibieien im Jahre 1876 gesammelt wurden. Sv. Vet.-Akad. Handl. 10(1): 1-62. 1885. Bryologische Fragmente. Hedwigia 26: 99-109; 129-169; 194-214. 1887.

typographically complicated system of Greek and Roman letters and numerals, indentations, asterisks, and daggers, is obscure and difficult to interpret. He described many new species, varieties, and forms, and gave formal recognition to every possible minor habitat variation. Although some of his descriptions are long and detailed, others are extremely meager and all are without definite measurements of any kind. Fortunately, most of his names have never been used for American plants, and so they need not be included in the synonymy here.

Boulay's treatment of Section *Harpidium* of *Hypnum* in *Muscinées de la France* (1884) was original and complete and the best monographic treatment of the group since the *Bryologia Europaea*. He collected the many scattered references to numerous species which had been proposed in the journals and pamphlets between 1866 and 1884 and put the material into workable form. His work is good because of its full detailed descriptions, excellent habitat notes, and comments on diagnostic features and relationships. With each revision of the group, more varieties appeared, and Boulay, no exception, proposed numerous new ones to add to the already long list.

Renauld's greatest contribution to the concept of the genus *Drepanocladus* was his indication of a variety or forma "typicum" for *Hypnum aduncum*, *H. fluitans*, and *H. revolvens*. Previously, no one had ever indicated the concept of a "typical" plant, which was rapidly being lost in the maze of varieties. I think it is safe to say that the modern concept of the genus begins with Renauld's work. His revision of Section *Harpidium* of *Hypnum* in Husnot's *Muscologia Gallica* (1894), supplemented by his numerous smaller papers,³ is extremely useful, as much for its notes of habit and relationships and its illustrations as for its taxonomic revision. His use of the ambiguous category "groupe" and "sous-groupe" often makes his nomenclature and classification obscure. Renauld retained many of Sanio's and Boulay's names and created many new, inadequately described varieties and forms.

Between 1875 and 1918 numerous local floras included treatments of the present genus *Drepanocladus*. In Berggren's *Musci et Hepaticae Spetsbergenses* (1875) several new varieties were proposed for these species, which he included under *Hypnum*. Lange and Jensen (1887) in their treatment of *Harpidium* in *Conspectus Florae Grønlandicae* gave full generic recognition to what had previously been a subdivision of *Hypnum*. The group, with new species, was included with *Amblystegium* by Lindberg and Arnell (1890) in *Musci Asiae Borealis* and Arnell and Jensen (1907) in *Die Moose des Sarekgebietes*. However, Bryhn (1906) in reporting the bryophytes of

³ Classification systématique de la section *Harpidium* du genre *Hypnum* de la flore française. *Rev. Bry.* 8: 73-82. 1881. Causerie sur les *Harpidia*. *Rev. Bry.* 33: 89-100. 1906; 34: 7-14. 1907. Notes sur quelques *Drepanocladus*. *Rev. Bry.* 36: 129-138. 1909; 37: 29-34. 1910.

the second expedition of the "Fram" and Hesselbo (1918), in *The Bryophyta of Iceland*, both considered the species in *Hypnum*.

The American publications of this period (Lesquereux and James' *Manual of the Mosses of North America* (1884) and Kindberg in Macoun's *Catalogue of Canadian Plants* (1892)) treated the group as the subgenus *Harpidium* of *Hypnum*.

Limpricht (1897-1898) in *Die Laubmoose Deutschlands, Oesterreichs, und der Schweiz*, includes 19 species in *Hypnum*, subgenus *Drepanocladus*, with full descriptions and measurements, and detailed distribution notes. Although every species is not illustrated, the pictures provided are clear and helpful.

Although Müller is responsible for the name *Drepanocladus*, Warnstorf, in his article "Die Europäischen Harpidien" was the first to use it as a genus and make the combinations.⁴ His article is important because of its comprehensive treatment which includes many new combinations as well as a historical survey of the literature, a general discussion of the relationships of the species, a key to the species, descriptions, and the distribution. Warnstorf (1906) followed his excellent and useful monograph with an equally fine treatment of *Drepanocladus* in *Kryptogamenflora der Mark Brandenburg*. His keys and descriptions are complete and detailed but of his 24 species, only 7 can be recognized as valid species; the remainder of his names have been reduced to either varieties or synonyms. Not only did he divide the genus into many species, but also he included innumerable varieties for each species. He, like Boulay, Renauld, and Limpricht, was a "splitter."

Roth (1905) in *Die Europäischen Laubmoose* treats 22 species of *Drepanocladus* with full descriptions, citations, and references. His treatment resembles Warnstorf's in that over half of his species are today recognized as merely varieties or habitat phases.

Loeske⁵ in an article "Drepanocladus, eine biologische Mischgattung" discussed the morphology of the group and its relationship to closely related genera and proposed the following names as genera. Although he indicated the species to be included, his new genera are *nomina nuda*, since he gave no descriptions of them.

1. *Sanionia*—*uncinata*, *orthothecioides*, *contigua*.
2. *Limprichtia*—*vernica*, *intermedia*, *revolvens*.
3. *Warnstorfia*—*exannulata*, *orthophylla*, *tundrae*, *purpurascens*, *fluitans* and varieties.
4. *Drepanocladus*—*aduncus* and varieties.
5. *Pseudocalliergon*—*turgescens*, *trifarum*, *longicuspis*.
6. *Scorpidium*—*scorpidioides*.

⁴ Beih. Bot. Centralbl. 13: 338-430. 1903.

⁵ Hedwigia 46: 300-321. 1907.

In his *Studien zur vergleichenden Morphologie und phylogenetischen Systematik der Laubmoose* (1910) he discusses these groups in more detail and supplements his statements of relationships among the species in the group. However, his names are still without generic descriptions.

Mönkemeyer's treatments of *Drepanocladus* in Pascher's *Süßwasser-Flora* (1914, 1931) and in *Die Laubmoose Europas* (1927) initiated the present tendency to reduce the number of species in the genus. There is no essential difference among his three publications; each includes the same eight species with keys, illustrations, and descriptions. Although he decreased the number of species, he included a large number of varieties and forms under each.

Brotherus, in "Die Laubmoose Fennoskandias" (1923) and in *Die natürlichen Pflanzenfamilien* (1925) adopted Mönkemeyer's policy of reducing the number of species and followed in large part his arrangement of varieties and forms. He used Loeske's proposed genera as sections and added section *Pseudo-Drepanocladus* for *Hypnum badium* Hartman.

Although writing as late as 1924, in *The Student's Handbook of British Mosses*, Dixon still included the species of *Drepanocladus* in *Hypnum*, subgenus *Harpidium*. His treatment follows Renauld's monograph with slight differences. The comments on distinguishing features, inter-specific and inter-varietal relationships, and habitats are his most valuable contribution.

The most recent treatment of *Drepanocladus* is Grout's in *Moss Flora of North America* (1931). As he states in his introduction, he has based his work on Renauld's and Mönkemeyer's published monographs and on their identified specimens.

As has been seen from the preceding synopsis, the concept of the genus *Drepanocladus* developed in Europe and most of the type localities are European. Because most of the species were described before the type concept was developed, types have never been designated. Under present world conditions it has been impossible to borrow material from Europe. However, the concept of the species has been so well developed in European and American literature and American herbaria that it has been possible to interpret American material from the descriptions, illustrations, and specimens. Because of the impossibility of studying European types and herbarium material, I have been forced to confine the scope of this monograph to North America. Therefore, only American material and names have been included; names which have never been used for American plants have not been considered.

MORPHOLOGY

Habit. The variability of *Drepanocladus* in habit, branching, and size depends largely on habitat conditions. *Drepanocladus uncinatus*, which most

frequently creeps over the ground, logs, or rocks, is irregularly or regularly pinnately branched. The stems of *D. aduncus* when growing among grass or reeds in swamps and marshes are creeping and fastigiately or irregularly pinnately branched. Submerged, floating stems are usually long, but may be either simple or regularly pinnately branched. Large, plumose fronds result when the stems are pinnate in the aquatic phase of *D. aduncus*, *D. fluitans*, or *D. exannulatus*. *D. uncinatus* var. *subjulaceus*, *D. exannulatus*, *D. brevifolius*, and *D. badius* often grow 5–8 cm. high, their stems erect, and simple or fastigiately branched. In bogs, *D. vernicosus*, *D. revolvens*, *D. aduncus*, *D. fluitans*, and *D. exannulatus* grow suberect in tufts and are fastigiately or irregularly pinnately branched. Sudden changes in environmental conditions may produce several long branch innovations near the tips of the stems.

Color. Although color is variable in *Drepanocladus*, it is reasonably characteristic for each species. *D. uncinatus* is from shining golden to yellow-green; *D. vernicosus* is light yellow-green; *D. aduncus* is from yellow-green to grass-green; *D. fluitans* is from dull yellow-green to brown; *D. exannulatus* is from crimson to red or purple; *D. revolvens* is from green to deep red or black and has a metallic sheen; *D. brevifolius*, *D. badius*, and *D. lycopodioides* are deep golden at the growing tips and brown or black below.

Stems. The apical buds of stems and branches are always pointed and are usually falcate-secund (except in *D. aduncus* var. *Kneiffii* and depauperate forms of *D. exannulatus*). However, in *Drepanocladus*, the apical buds are never cuspidate as is characteristic in the closely related genus, *Calliergon*.

The stems of *Drepanocladus* generally lack paraphyllia and radicles. Pseudoparaphyllia are produced in the axils of the branches of *D. uncinatus*. Some plants of *D. fluitans* and *D. badius* produce radicles from the apex, base, margin, or costa of the leaves.

The stems of all the species of *Drepanocladus* (except *D. vernicosus* in which the central strand is lacking) show in cross section a small central strand of 3–6 cells embedded in a loose ground tissue. The 2–3 rows of cortical cells may or may not be incrassate or colored. The outer layer of cortical cells of *D. revolvens* is enlarged. Stems vary in diameter from 2–6 mm.

Leaves. Although the leaves of *Drepanocladus* are typically falcate, and may further be strongly and regularly circinate (*D. uncinatus* and *D. revolvens*), they are straight in *D. aduncus* var. *Kneiffii* and the short-celled environmental phases of *D. fluitans* and *D. exannulatus*. In submerged

plants the curvature of the leaves is decreased and the acuminations are long, lax, and twisted. The strongly falcate leaves of *D. aduncus*, *D. fluitans*, and *D. exannulatus* are channelled at the apex, whereas the straight leaves of some of their varieties have a flat apex.

The leaves of *Drepanocladus* range from strongly and regularly plicate, through irregularly plicate and striate, to completely plane. *D. uncinatus* is the only species of the genus with strongly regularly plicate leaves; the plications are distinctive because each fold extends continuously from the base of the leaf to the apex. The leaves of *D. vernicosus* are plicate only in the broadened basal part, with the apex flat. Forms of other species (*D. exannulatus*, *D. fluitans*, and *D. aduncus*) may become irregularly striate or sulcate in response to certain environmental conditions. This and similar characters, resulting from habitat conditions, are usually not constant on any plant. In the other species, *D. revolvens*, *D. lycopodioides*, *D. badius*, and *D. brevifolius*, the leaves are not folded in any way; they are plane or concave.

The shape of the leaves of *Drepanocladus* varies from broadly oval to linear-lanceolate. Leaves of small plants of *D. aduncus* are broadly ovate; leaves of *D. aduncus* var. *Kneiffii*, *D. badius*, *D. lycopodioides*, *D. brevifolius*, *D. fluitans*, and *D. exannulatus* are broadly lanceolate; leaves of *D. exannulatus* and aquatic plants of *D. aduncus* are long lanceolate; leaves of aquatic plants of *D. fluitans* are linear-lanceolate.

The acumination may be short and abrupt or long and gradual. Half the length of the leaf of *D. uncinatus* is the long, subulate acumen. The acumination of *D. vernicosus* is abrupt and broad. The leaf of *D. revolvens* is gradually narrowed until within 0.3–0.5 mm. of the apex where it is rapidly narrowed to a filiform point. Forms with ovate or broadly lanceolate leaves are usually abruptly short-acuminate whereas forms with long-lanceolate or linear-lanceolate leaves are gradually long-acuminate. In general, long leaves with long acuminations are produced by complete submergence.

The leaves of all the species of *Drepanocladus* clasp the stem, and are erect rather than spreading. The alar region of the leaf may or may not be decurrent. As a result of variation in decurrency, the line of insertion of the leaf varies from truncate, through broadly or narrowly concave to circular. The alar cells of *D. aduncus* are decurrent, therefore the base of the leaves is always concave. Whether the line of insertion is widely or narrowly concave depends upon the width of the leaf at the base, the diameter of the stem, and the degree of decurrence of the alar cells. Since the alar cells of *D. fluitans* and *D. exannulatus* are not decurrent, the base of the leaf is truncate. The few quadrate alar cells of *D. uncinatus* are slightly decurrent, thus forming a shallowly concave line of insertion seen when the leaves are

removed from the stem. Leaves of *D. revolvens*, *D. badius*, *D. vernicosus*, *D. brevifolius*, and *D. lycopodioides* with quadrate cells across the entire base are always truncate.

The margin of the leaves of *D. aduncus*, *D. vernicosus*, *D. revolvens*, *D. lycopodioides*, *D. badius*, and *D. brevifolius* is entire or sinuate at the base. The leaf margins of *D. exannulatus* and *D. fluitans* are serrulate at the base or apex or both. The long subulate acumination of *D. uncinatus* is distinctly serrulate while the base is entire or only slightly serrulate. Whether the serrulations are distant or close depends upon the length of the cells.

Costa. The leaf costa or nerve of *Drepanocladus* is almost universally single, not forking or double (except in *D. fluitans* var. *Berggrenii*); it varies in length and width. In depauperate forms of *D. aduncus* and *D. fluitans* it is short ($1/3$ – $1/4$ the length of the leaf) and weak (12–20 μ in diameter at base). In *D. vernicosus*, *D. uncinatus*, *D. revolvens*, *D. exannulatus*, and *D. fluitans* it is long ($1/2$ – $5/6$ the length of the leaf) and strong (40–80 μ wide at the base). In *D. aduncus* var. *capillifolius* and *D. exannulatus* var. *Rotae* the costa is long-excurrent and 80–150 μ wide at the base, and usually deeply colored. Submerged plants of *D. aduncus* and *D. exannulatus* may develop a wide, deeply colored costa. In all species of *Drepanocladus*, including the varieties with excurrent costa, it is tapering.

The cells of the costa are narrowly linear, and usually longer than the cells of the lamina of the leaf. With the exception of *D. vernicosus*, the costa as seen in cross-section is biconvex with a small central strand. The costa of *D. vernicosus*, like the stem, has no central strand.

Areolation. The leaf cells of *Drepanocladus* are narrowly linear, with the exception of certain habitat phases of *D. aduncus*, *D. fluitans*, and *D. exannulatus*, in which the median leaf cells are oblong (4–6 $\mu \times 28$ –32 μ). Cells are longest in *D. fluitans* and *D. exannulatus* (4–6 $\mu \times 60$ –100 μ) and shorter in *D. aduncus*, *D. revolvens*, *D. vernicosus*, and *D. uncinatus*. In general the cells are uniform in size and shape throughout the leaf, being only slighter shorter and broader toward the base in *D. aduncus*.

The cell walls are thin in *D. aduncus*, *D. fluitans*, *D. uncinatus* and *D. vernicosus*. In some plants of *D. exannulatus* and *D. aduncus* the walls of basal and alar cells are deeply colored. Basal cells of *D. revolvens* and *D. lycopodioides* are pitted, whereas all cell walls in *D. badius* and *D. brevifolius* are porose. In *D. revolvans* only the basal cell walls are incrassate; in *D. badius* and *D. lycopodioides* all cell walls are incrassate and deeply colored brown or red.

The alar cells of *Drepanocladus* may be large and inflated, small and quadrate, hyaline or colored, thin-walled or incrassate, entire or porose, or any combination of these. In *D. aduncus* the alar cells are inflated and

hyaline, forming distinct auricles extending $1/4-1/3$ the distance from the margin to the costa. Only in extremely robust submerged plants are the basal and alar cells colored in *D. aduncus*. In *D. fluitans* the alar cells are slightly inflated and extend $1/4-1/3$ the distance from the margin to the costa. The alar cells of *D. exannulatus* are always large, but may be thin-walled or incrassate, hyaline or colored, and form either large triangular groups extending to the costa or a single row of elongated cells across the entire base. The alar cells of *D. badius* are inflated, incrassate, and porose. *D. uncinatus* has a small group of quadrate, hyaline alar cells. The alar cells of *D. vernicosus*, *D. revolvens*, *D. lycopodioides*, and *D. brevifolius* are not differentiated at the basal angles, although there are two or more rows of shorter cells (hyaline and thin-walled in *D. vernicosus*; incrassate, porose, and colored in *D. revolvens*) across the entire base of the leaf. In general, if the alar cells are large and inflated they are thin-walled; and if they are incrassate they are smaller.

The incrassate cell walls between any two basal cells of *D. revolvens* are $4\ \mu$ thick, usually with 1-3 pits. The two secondary cell walls between two alar cells are $4-8\ \mu$ thick in *D. revolvens*, *D. badius*, and *D. lycopodioides*.

Alar cells differ not only in their size and shape but also in their spatial relationship with the other cells of the leaf. The alar cells of *D. aduncus* and *D. fluitans* intergrade completely with the cells of the lamina of the leaf and the transition is imperceptible. However, in *D. aduncus* the alar cells are ventricose and oriented in a different plane from the other leaf cells so that the alar cells are sharply delimited from the cells of the lamina. The alar cells of *D. exannulatus* and *D. fluitans* are never ventricose nor placed at an angle. *D. exannulatus*, unlike *D. fluitans*, shows an abrupt transition from the alar cells to the cells of the lamina so that the alar region is sharply delimited by the size of the cells.

When leaves of *D. fluitans*, *D. exannulatus*, and *D. aduncus* are removed from the stems, usually some of the cortical stem cells remain attached to the base of the leaves as long "tails." This does not occur so often in *D. vernicosus*, *D. uncinatus*, *D. revolvens*, *D. badius*, *D. brevifolius*, or *D. lycopodioides*. One of the differences distinguishing *D. aduncus* from *D. fluitans* and *D. exannulatus* is the transition from the stem cells to the leaf cells; in *D. aduncus* it is gradual, whereas in *D. fluitans* and *D. exannulatus* it is abrupt.

Perichaetium. In all species of *Drepanocladus* the perichaetium sheaths the base of the seta. The outer perichaetial leaves are spreading, from ovate to broad-lanceolate, and either ecostate or with a short costa. The inner perichaetial leaves are costate, long-lanceolate, and from gradually or abruptly acuminate to piliform. The perichaetial leaves of *D. uncinatus*, like the vegetative leaves, are regularly and strongly plicate and serrulate at the

apex. In other species, the perichaetial leaves are smooth or irregularly striate, and entire or serrulate.

Perigonial leaves. The perigonial leaves of all species of *Drepanocladus* are similar. They are ovate, abruptly short-acuminate, with a short costa or ecostate, serrulate or entire.

Sporophyte. The capsule and peristome of *Drepanocladus* are typically Hypnaceous. With the exception of the erect symmetric capsule of *D. uncinatus* var. *symmetricus*, the capsule of all species is asymmetric and curved; it may be plicate or smooth. The exothecial cells are smooth or mamilllose. The operculum is rostrate or apiculate, attached in all species (except *D. fluitans* and *D. exannulatus*) by a persistent annulus of 2–3 rows of cells. The peristome is perfect, that is, with sixteen teeth and sixteen segments and alternating cilia. The sixteen teeth are transversely thickened and longitudinally striate. The segments of the inner peristome are longitudinally striate with 2–3 cilia.

PHYLOGENY

Drepanocladus belongs to the subfamily Amblystegieae, which includes all the Hypnaceae which have a single costa and a long arcuate-cylindric capsule.

Generic relationships. *Drepanocladus* is most closely related to *Scorpidium*; in fact, the relationship is so close that they have been grouped together by many bryologists. One species of *Scorpidium* is recognized today—*S. scorpioides*. Milde⁶ placed it in the subgenus *Harpidium* with the present species of *Drepanocladus*, and Warnstorff⁷ called it *Drepanocladus scorpioides*. *Scorpidium* has all the characteristics of the genus *Drepanocladus* except that the leaf apex is obtuse or apiculate and the costa is faint, short and double, or lacking. To the naked eye, the two genera are so similar that *Scorpidium scorpioides* resembles a very large *Drepanocladus*.

Although *Calliergon* differs from *Drepanocladus* in its straight leaves and rounded or cucullate apices, the close relationship between the two genera is shown not only in their similarity of areolation and costa, but also by their parallel series of species. The same modifications of alar cells, cell walls, costae, and leaves that separate the species of *Drepanocladus* likewise distinguish the species of *Calliergon*. The two genera occur in the same range and in the same types of habitats and are often found associated.

Calliergidium, intermediate between *Drepanocladus* and *Calliergon*, seems to be an artificial genus. One of its species, *C. pseudostramineum*, is

⁶ Bryologia silesiaca, p. 350. 1869.

⁷ Kryptogamen-Flora der Mark Brandenburg und angrenzender Giebete. 2: 1027. 1906.

so closely related to *Drepanocladus* that Warnstorf⁸ and Brotherus⁹ have considered it a form of *D. fluitans*. Grout¹⁰ has considered the erect and straight leaves with blunt apices sufficiently distinctive to separate *C. pseudostramineum* from *Drepanocladus*. In general habit, the plants named *D. pseudostramineum* I have seen have resembled *Calliergon* more than *Drepanocladus*. Further collections of these two species, will, I believe, dispense with this artificial genus and place its species in *Drepanocladus* and *Calliergon*.

In a phylogenetic arrangement, *Drepanocladus* and *Calliergon* form a related species-complex to which the other members of the subfamily are less closely allied.

The species of *Hygrohypnum* with falcate, acuminate leaves and a single costa superficially resemble the species of *Drepanocladus*. However, the species with straight, blunt leaves and short, double costae are never confused with *Drepanocladus*. Furthermore, *Hygrohypnum*, *Hygroamblystegium*, and *Leptodictyum* grow most frequently in running water, whereas *Drepanocladus* occurs usually in still water. *Hygrohypnum* is so variable and heterogeneous a group that it is difficult to determine its relationship to other genera.

Cratoneuron, in spite of its falcate leaves, decurrent alar cells, and single costa, is distinctive from *Drepanocladus* because of its numerous paraphyllia. It is the only genus in the subfamily which has developed paraphyllia and it therefore holds a unique place in the phylogeny of the Amblystegieae.

Hygroamblystegium is separated primarily from *Amblystegium* on the basis of its aquatic habitat. On the same basis it is more closely allied to and more often confused with *Drepanocladus* than is *Amblystegium*. However, any similarity between *Hygroamblystegium* and *Drepanocladus* is only superficial, for the robust habit, erect-spreading, non-falcate leaves, and thick-walled rhomboidal leaf cells distinguish *Hygroamblystegium*.

Leptodictyum, like *Hygroamblystegium*, resembles *Drepanocladus* only superficially in its aquatic habitat. The leaves are never falcate, but are always erect or erect-spreading, and the alar cells are never inflated. These characters distinguish species of *Leptodictyum* from *Drepanocladus aduncus* var. *Kneiffii*, the only *Drepanocladus* to which it shows any similarity.

Plants of *Amblystegium* or *Campyllum* with falcate leaves are sometimes confused with small plants of *Drepanocladus*. *Campyllum*, with its typically squarrose-recurved, broadly ovate or lanceolate leaves, is unlike any species or variety of *Drepanocladus*. *Amblystegium* is distinct in its short leaf cells, erect-spreading leaves, and quadrate or only slightly inflated alar cells.

⁸ L.c., p. 1040.

⁹ Die Laubmoose Fennoskandias 1: 479. 1923.

¹⁰ Moss flora of North America north of Mexico 3(2): 100. 1931.

Interspecific relationships. The origin of the species of any group is a speculative but nevertheless an interesting and significant problem. From the comparative morphology of the species of *Drepanocladus*, it is possible to deduce the relationships and to postulate the origin of the species of the genus.

Two general trends of development in the genus have been (1) the production of inflated cells, and (2) the production of alar cells which are not inflated, but which may be differentiated in other ways (see figure 1).

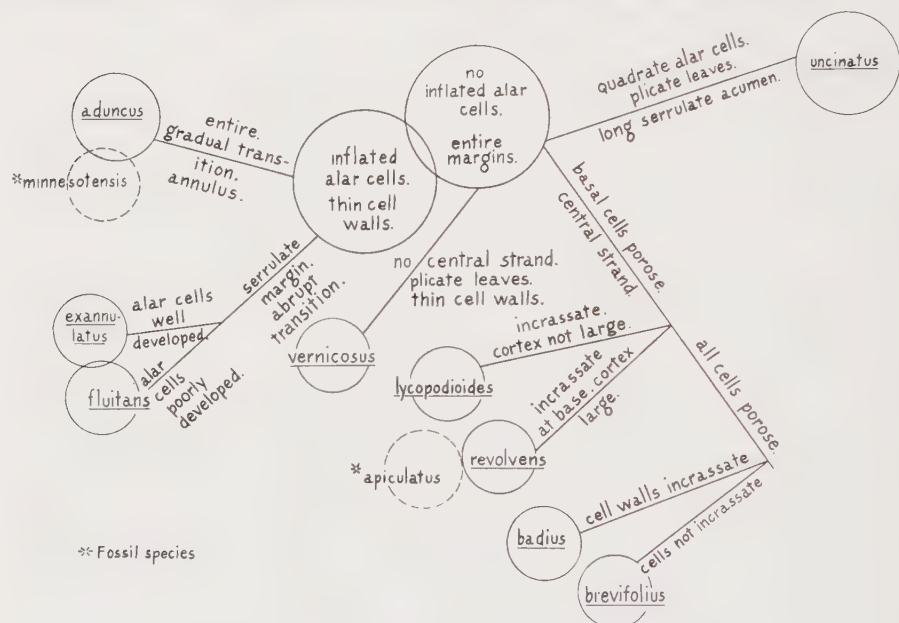


FIG. 1. Inter-relationships of the species of *Drepanocladus*.

Drepanocladus aduncus, *D. fluitans*, and *D. exannulatus* have inflated alar cells and are obviously closely related. An early ancestor must have furnished to all three species the inflated alar cells, and thin cell walls which are not pitted. Subsequent segregation of traits gave rise to (1) *D. aduncus* with entire margins and a gradual transition from the cortical stem cells to the leaf cells, and to (2) *D. fluitans* and *D. exannulatus* with serrulate margins and an abrupt transition from cells of the stem to the cells of the leaf, and the annulus lacking on the capsule. Further evolution has segregated *D. fluitans* with its delicate habit and its poorly developed alar cells which intergrade completely with the cells of the lamina, and *D. exannulatus* with its robust habit and its well developed, clearly delimited alar cells extending across the entire base of the leaf.

Development of the three species, *D. fluitans*, *D. exannulatus*, and *D. aduncus* must have been parallel, because the series of varieties in each is

similar. These three species respond to the same environmental conditions with the same modifications. Each species when growing submerged produces longer stems, longer leaves at greater intervals on the stems, longer leaf cells, and regular pinnate branching. Each species also produces a short-celled, short-leaved phase when it grows in certain unfavorable conditions. Although the variety with an excurrent costa is lacking in *D. fluitans*, it is present in both *D. aduncus* (var. *capillifolius*) and *D. exannulatus* (var. *Rotae*). *D. aduncus*, unlike *D. fluitans* and *D. exannulatus*, produces a variety with straight leaves (var. *Kneiffii*).

The other evolutionary trend, the production of alar cells which are not inflated, gave rise by various combinations of characters to the other species of the genus. Any postulation of the order in which these forms were produced would be pure speculation. *D. vernicosus*, *D. revolvens*, *D. brevifolius*, and *D. lycopodioides* are similar in the absence of any differentiated cells at the basal angles of the leaf, and in the presence of several rows of differentiated cells across the entire leaf base. *D. vernicosus*, the only species in the genus without a central strand, is distinct in its stem structure, and in its characteristically plicate and abruptly acuminate leaves with thin-walled cells.

Drepanocladus revolvens and *D. lycopodioides* may have developed from the same stock. *D. revolvens* has only the basal cells incrassate and pitted, whereas, in *D. lycopodioides*, all the cell walls are incrassate with the basal cell walls very thick and porose. The tendency toward incrassate, porose cell walls, partially developed in *D. revolvens*, is intensified in *D. lycopodioides*. The two species differ slightly in stem structure; the outer layer of cortical cells in *D. revolvens* is enlarged, whereas all the cortical cells are of the same size in *D. lycopodioides*. In habit and leaf shape the two species are similar except that *D. lycopodioides* is larger and more robust than *D. revolvens*.

Drepanocladus brevifolius and *D. badius* developed the same cell-wall modifications to produce plants in which all the leaf cells are porose. In *D. brevifolius* the cell walls are uniform in thickness and not, or only slightly, incrassate, whereas in *D. badius* all cell walls are incrassate with the basal cells especially strongly thickened. There are minor differences between the two species in the alar cells: in *D. brevifolius* there are no differentiated alar cells, but some leaves have a row of slightly inflated cells across the insertion of the leaf; *D. badius* always has some differentiated cells, either at the basal angles or across the entire base of the leaf.

Drepanocladus uncinatus is so distinct from all the other species of the genus that it seems probable that it developed along a separate line from the other members of the group. It has neither the inflated alar cells of *D. aduncus*, *D. fluitans*, or *D. exannulatus*, nor has it the basal row of dif-

ferentiated cells characteristic of *D. vernicosus*, *D. revolvens*, and *D. lycopodioides*. Instead, a group of quadrate alar cells is always present. The regular, long plications and the long, subulate, serrulate acumen are characteristic of *D. uncinatus*. Not only is *D. uncinatus* distinctive in its diagnostic features, but also in its habitat. It is the only species of *Drepanocladus* which is xerophytic or mesophytic rather than hydrophytic. In fact, *D. uncinatus* is so distinct that Loeske created the genus *Sanionia* for *D. uncinatus* and its varieties (see above).

From *D. uncinatus* developed the var. *symmetricus* with erect symmetric capsules but otherwise with the gametophytic characters of the species; this variety is restricted in its range to the western part of North and South America.

VARIATION IN DREPANOCLADUS

The species of *Drepanocladus* are well defined and have been known for a long time. On the other hand, the many forms and varieties which have been proposed for some of the species have been poorly defined and troublesome for taxonomists. I believe that lack of understanding of the variation in the genus is responsible for the taxonomic dilemma which confronts bryologists working in it.

Variation is of two sorts: that which is initiated by environment and that which is based on heredity. Botanists have confused these two types of variation in many groups of plants, including *Drepanocladus*.

American bryologists have recognized that species of *Drepanocladus* respond to changes in environment to a startling degree. Grout¹¹ states: "In 1929, in a pond not far from Cold Spring Harbor, was collected *Drepanocladus fluitans gracilis*. In 1931, when the water was low, there was a vigorous emergent growth, the upper leaves of which were typical *D. fluitans Jeanbernati*, while the lower leaves, grown apparently while submerged, were those of var. *gracilis*. On some of the shoots were leaves nearly typical of *D. fluitans* proper. This seems to show that in *Drepanocladus*, at least, habitat conditions modify structure profoundly." Conard¹² investigated the same pond in 1933 and 1934 and found the same conditions to exist: "In wet seasons this moss is the var. *gracilis*, but in dry seasons it becomes var. *Jeanbernati*." I have not recognized these two so-called varieties, *Jeanbernati* and *gracilis*, because they, along with many others, are merely environmental fluctuations.

Sporophyte characters are of little value in determining species of *Drepanocladus*. With the exception of *D. fluitans* and *D. exannulatus* which have no annulus on the capsule, and *D. uncinatus* var. *symmetricus* which

¹¹ Miscellaneous notes on mosses. *Bryologist* 36: 25, 26, 1933.

¹² The plant associations of Central Long Island—A study in descriptive plant sociology. *Am. Mid. Nat.* 16: 433-516, 1935.

has an erect instead of cernuous capsule, the sporophytes of all species of *Drepanocladus* are identical. Gametophyte characters, therefore, must be used for classification and identification. Great variation in habit, color, branching, leaves, costae, and areolation has led to the publication of many varietal and formal names for extreme plants produced by extreme environmental conditions. Because the most variable species of *Drepanocladus*, *D. aduncus*, *D. fluitans*, and *D. exannulatus*, have responded to different environments with similar modifications, a long series of variety and form names have been proposed for each of the species. Most of these subspecific names were first proposed under *Hypnum*; many of them were never transferred to *Drepanocladus*. Submerged plants of *D. aduncus* have been called var. *aquaticum*, *larifolium*, *pseudofluitans*, and *larum*; of *D. fluitans*, var. *submersum*; of *D. exannulatus*, var. *longifolium*. Small forms of these three species have been given variety and form names such as *gracilescens*, *tenue*, *attenuatum*, *filiforme*, *brevifolium*, *tenellum*, *condensatum*, and *abbreviatum*. Deeply colored plants have been called var. *purpurascens*. Short-celled leaves have been called *polycarpon* and *brachydictyon*. Every possible environmental variation has been named.

When the true nature of variation in *Drepanocladus* is understood, it is possible to eliminate these innumerable varieties which cannot be described nor recognized. The result of such a procedure is that only a few subspecific names remain and these are varieties which are hereditary.

In spite of the fact that bryologists have long recognized that much of the variation in *Drepanocladus* was due to environmental conditions, no attempt has heretofore been made to restrict varieties to hereditary variation. I have given varietal rank only to those variations which appear to be hereditary; environmental fluctuations have been discussed so that they may be recognized as such, but will not be included in the formal taxonomy. When a character is constant in all parts of a plant, regardless of environment, it is apparent that its uniformity is the result of fundamental genetic factors. When a certain character differs on different parts of the same plant—for instance, leaves from different parts of the stem—it is obviously influenced by environmental conditions.

Field and herbarium studies were made to determine which characters were modified by changes in the environment and which remained constant through a changing environment. It was discovered that genetic factors determined (1) whether the costa was excurrent or short and (2) whether the leaves were falcate or straight. Combinations of these two hereditary characters produce three varieties in *D. aduncus*: var. *typicus* with falcate leaves and a short costa; var. *Kneiffii* with straight leaves and a short costa; and var. *capillifolius* with falcate leaves and an excurrent costa. In *D. exannulatus* the leaves are always falcate but the length of the costa varies.

Therefore I have recognized var. *typicus* with a short costa and falcate leaves and var. *Rotae* with an excurrent costa and falcate leaves.

Other characters, such as cell size and leaf length, are influenced by the environment and may vary on the same plant. In *D. aduncus*, *D. fluitans*, and *D. exannulatus* two habitat phases result from this type of variation: (1) short leaves and broad, oblong-linear cells; and (2) long, flexuose, widely-spaced leaves and long-linear cells. These phases may be found on the same plant, and they may be produced on any of the varieties. Leaves on the lower, and submerged portion of the stem of any of these species may be the aquatic phase (2) while the upper, emergent part of the same stem may be either typical or short-celled (1). However, if the lower, submerged leaves have an excurrent costa, the upper ones will have an excurrent costa also, though the cells may be different. Therefore, since the costa is the constant character, it is apparent that the length of the costa is controlled by genetic factors, while the leaf and cell size are conditioned by environmental factors. Falcate leaves are an expression of hereditary factors, for, if the leaves are falcate in one part of the stem, they will be falcate throughout, even though submerged or subjected to other modifying environmental conditions.

Environmental conditions producing habitat forms in *Drepanocladus*.

The same habitat conditions produce similar forms in *D. fluitans*, *D. exannulatus*, and *D. aduncus*.

Zastrow¹³ carried out controlled experiments on mosses and compared growth submerged and emergent under identical conditions of pH. She found that, in general, growth under water led to pinnate branching, longer leaves, longer leaf cells, larger and more numerous alar cells, widely spaced leaves, and a weaker costa. These modifications are produced by submerged plants of *D. aduncus*, *D. fluitans*, and *D. exannulatus*.

The short-celled variation often seen in *Drepanocladus* occurs most commonly on the emergent stems of plants growing in water. However, this form appears to be the result of recent flooding. Apparently the form is produced when the plant has more water available than is customary in its habitat. When the water supply is abundant and constant, all the leaves are similar and characteristic of submerged growth. When the water supply fluctuates, different forms are produced on the same plant under the different conditions; one of the forms produced under these conditions is invariably the short-celled phase of *D. aduncus*, *D. fluitans*, or *D. exannulatus*. Consequently, plants growing in deep lakes are entirely the submerged phase, whereas plants which grow in temporary ponds and pools and intermittent streams produce the short-celled variation on part of their stem.

¹³ Experimentelle Studien über die Anpassung von Wasser- und Sumpfmossen. Pfl.-Forsch. 17: 1-70, 1934.

Field studies around the Huron River, Washtenaw County, Michigan, indicated this type of environmental fluctuation first in 1940. On May 14, when the water level in a pond near the river was high, plants which had produced the short-celled leaves on the emergent stems were collected (Wynne 1701). In the summer (June 30) when the pond was stagnant and the water level stable, all the new growth was the aquatic phase (Wynne 1712). On August 30 collections again showed that short-celled leaves had been produced by a rise in the water level (Wynne 2072). Later (October 15) and until winter the conditions remained stable and all the leaves produced were of the aquatic type (Wynne 2230). Similar reactions were observed in Reese's Bog, Cheboygan County, Michigan. June 29, 1942, with much water in the bog, the leaves on the growing stems were short-celled (Wynne 2453). With less water (July 30) the plants were producing typical leaves (Wynne 2591).

The evidence obtained from these and many similar field observations was substantiated by large herbarium collections and extensive field notes from Quebec by H. Dupret. Many of Dupret's collections are in series from the same locale taken at different dates. When the response of each species to environmental changes was known, then each plant told its own history. By examining leaves from different parts of a stem of *Drepanocladus*, it is possible to tell approximately under what environmental conditions those leaves were produced. This knowledge made possible the interpretation of herbarium specimens and the elimination of environmental fluctuations from the formal nomenclature in the genus.

Statistical studies. In order to understand the variation in the genus *Drepanocladus*, statistical studies, as well as field studies, were made of the variable species. Measurements were made of all diagnostic features including serrulation, acumination, size, attachment, decurrency, and distance apart of the leaves; size of cells at base, alar region, margin, and apex of leaves. By plotting the results, it was easy to see whether the population fell naturally into one or several units. This information was useful in determining whether or not certain varieties were valid.

Figure 2 shows the statistical evidence that was used in determining the varieties in *D. revolvens* and *D. uncinatus*. All collections of *D. uncinatus* were examined and measured and the length of the leaf was plotted on a single histogram. Two populations were then apparent: one with leaves 2.0–4.0 mm. long and another with leaves 4.4–5.5 mm. long. Previous to this study several varieties, called *plumulosum*, *abbreviatum*, *plumosum*, *gracilescens*, and *gracillimum*, had been separated because of shorter leaves and a more delicate habit. When these simple statistical studies indicated that such a separation was artificial, a further, more careful examination of

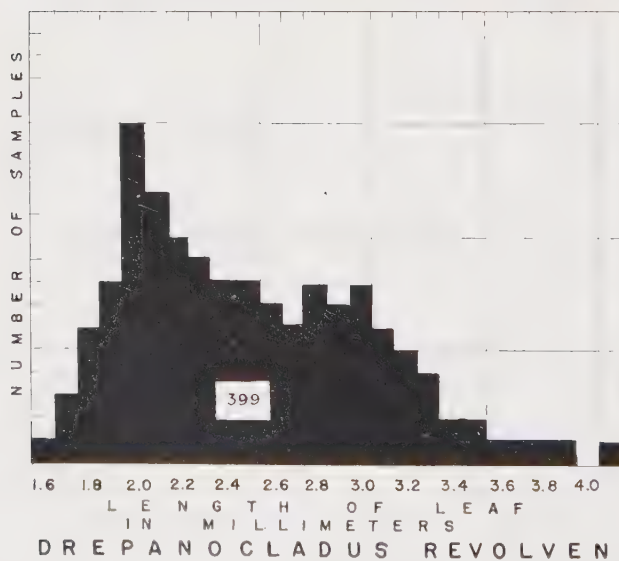
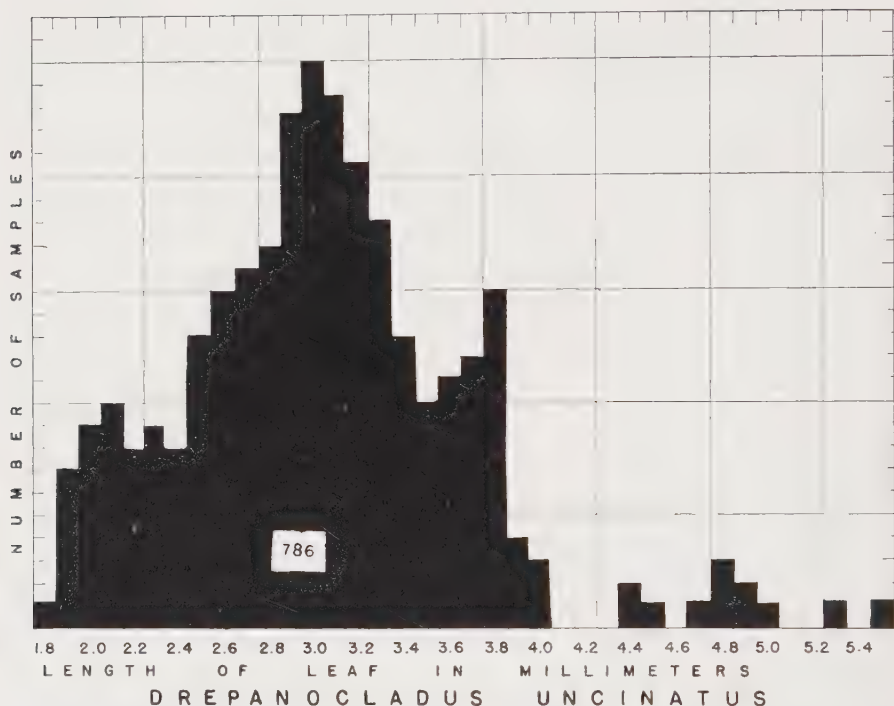


FIG. 2. Statistical data on *Drepanocladus uncinatus* and *D. revolvens*.

collections so named was made. In all these collections leaves of various lengths (2.2, 2.4, 2.5, 3.0, 3.2 mm.) were found in the same clone. The author believes, therefore, that small leaves are minor habitat variations of a large variable population, *D. uncinatus* var. *typicus*. The small group of plants with leaves 4.4–5.5 mm. long belong to *D. uncinatus* var. *subjulaceus*. The large size of the leaves on these plants is constant and correlated with a robust habit, a golden yellow color, and a distinct geographical range (western North America and Quebec and Newfoundland).

Length of leaf and length of acumination of plants known as *D. revolvens* and *D. intermedius* were measured and plotted on the same histogram. This indicated that *D. intermedius*, which had been separated from *D. revolvens* on the basis of its smaller leaves and shorter acumination, was not a natural population. Furthermore, examinations of many leaves from the same plant revealed acuminations varying in length from 0.1 to 0.8 mm. Therefore, on the basis of these observations, the name *D. intermedius* (Lindb.) Warnst. has been excluded and plants previously called *D. intermedius* placed in *D. revolvens*.

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Studies in Drepanocladus. II. Phytogeography

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Frances E. Wynne

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General Distribution of Drepanocladus

World distribution.—*Drepanocladus* has a circumpolar distribution in both hemispheres. In the northern hemisphere it occurs throughout arctic and northern North America, Europe, and Asia. In the southern hemisphere it has been collected in the Andes, southern South America, New Zealand, and Australia. However, *Drepanocladus* is notably lacking in all tropical climates.

Distribution in the northern hemisphere.—*Drepanocladus* is a characteristic plant of alpine meadows and of arctic and boreal swamps and bogs, and occurs in arctic regions in the Aleutian Islands; Alaska; Ellesmere, Grinnell, Devon, and Baffin Islands of the American Arctic Archipelago; Labrador; Greenland; Iceland; in Europe in Scandinavia, Spitzbergen, Bear Island; in Asia in Franz Joseph Land, Nova Zembla, the whole Siberian mainland, and Kamchatka. *Drepanocladus* extends southward in North America to California, Nevada, Utah, New Mexico, Mexico, Nebraska, Missouri, Illinois, Indiana, West Virginia, and New Jersey; in Europe the genus extends south in the Pyrenees, the Swiss Alps, the Balkans, and the Caucasus; and in Asia in the Himalayas. As *Drepanocladus* extends farther south it disappears in the lowlands, and occurs only at high altitudes in the mountains.

Flowering plants with similar distribution.—Similar circumpolar distributions occur among the flowering plants, for example: *Deschampsia caespitosa* (L.) Beauv. has been reported from Greenland; arctic and temperate North America, Asia, and Europe; southern South America; Tasmania; and New Zealand; and *Heirotchloë alpina* (Schwartz) Roem. & Schult. from North America, the mountains of New England; eastern Asia, the mountains of central Asia; Australia; and New Zealand.

Classification of Species of *Drepanocladus*

Geographical.—The species of *Drepanocladus* may be classified geographically into two groups—arctic-alpine and boreal-montane. The arctic-alpine species are *D. badius*, *D. brevifolius*, *D. fluitans* var. *Berggreni*, and *D. lycopodioides*; the boreal-montane species are *D. aduncus*, *D. fluitans*, *D. exanulatus*, *D. revolvens*, *D. vernicosus*, and *D. uncinatus*.

The arctic-alpine species (map 1) are more restricted in their range than the boreal-montane species, which may be due as much to imperfect knowledge as to the actual distribution of the plants. The boreal regions have been relatively more thoroughly explored for plants than the arctic regions. This accounts for the small number of collections of the arctic-alpine species. However, the fact that the arctic-alpine species have never been collected in the well explored boreal regions indicates that their range is actually restricted to the extreme north where they undoubtedly occur more frequently than they have been collected. *Drepanocladus fluitans* var. *Berggreni* is known from



Map 1. World distribution of the arctic-alpine species of *Drepanocladus*. Map 2. World distribution of the boreal-montane species of *Drepanocladus*. Reprinted by permission from "Outline Maps and Graphs" by R. B. Hall, published by John Wiley & Sons, Inc.

arctic Norway, Sweden, Greenland, and Ellesmere Island. *Drepanocladus brevifolius* and *D. badius* have been collected most often of the arctic-alpine species; they have been found in Siberia, Spitzbergen, Bear Island, Greenland, and arctic America. *Drepanocladus badius* occurs also in northern Scandinavia and Labrador and in the islands northward.

The boreal-montane species (map 2), *D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. vernicosus*, *D. revolvens*, and *D. uncinatus*, are widespread in the arctic regions; nevertheless, they are most abundant in more temperate climates where they occur in boreal bogs and swamps and along the mountain ranges. These six species are found in arctic Europe and Asia and occur as far south as the alps in Europe. In addition, *D. exannulatus* is found in the Caucasus and the Himalayas; *D. fluitans* occurs in the Pyrenees and the higher mountains of the Canary Islands; and *D. aduncus* has been reported from the Caucasus.

In eastern North America the boreal-montane species of *Drepanocladus* occur from the arctic southward to New Jersey, West Virginia, Ohio, Illinois, and Missouri. In western North America the southern limits of the boreal-montane species of *Drepanocladus* are in the mountains of Nebraska, New Mexico, Utah, Nevada, California, and Mexico.

Genetical.—The species of *Drepanocladus* are rather sharply divided into two categories on the basis of fundamental variability. Some species are extremely adaptable and respond to the slightest change in environmental conditions. So great is the adaptability that on one plant, leaves produced at different times under different conditions vary so greatly that they could be placed in separate varieties if it were not known that they came from the same stem. In contrast to the variable species, the stable species of *Drepanocladus* are clear-cut and well-defined.

The correlation between the stable and the arctic-alpine species (*D. badius*, *D. brevifolius*, *D. lycopodioides*, and *D. fluitans* var. *Berggreni*) and the variable and the boreal-montane species (*D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. revolvens*, *D. vernicosus*, and *D. uncinatus*) is striking. This division is exactly what one would expect from a consideration of the ranges of the species of *Drepanocladus*. The stable arctic-alpine species are limited to one region and to one type of habitat. The variable boreal-montane species, however, tolerate a wide variety of habitats and consequently have spread over a wider range.

Even within the boreal-montane group, the variability of each species correlates with its distribution. *D. fluitans*, *D. exannulatus* and *D. aduncus* are extraordinarily variable and respond to every change in the environment. Of these, *D. aduncus* is the most variable and adaptable, and therefore is the most widespread geographically. It has a continuous distribution in North America, extends across the entire northern part of the continent, and ranges farther south than any other species of *Drepanocladus* to New Mexico, North and South Dakota, Nebraska, and Missouri. *D. fluitans* is most common in eastern North America where the very wet habitats it requires are most abundant. *D. exannulatus* is frequent in eastern North America and in the western mountains. Both *D. fluitans* and *D. exannulatus* are completely lacking in the

plains of the central part of the continent. Apparently they are unable to resist periods of dryness and cannot live, with *D. aduncus*, in the intermittent streams and ponds of central North America.

Of the boreal-montane group, *D. revolvens*, *D. vernicosus*, and *D. uncinatus* are the most clear-cut species. Of these three, *D. vernicosus* has been collected least frequently. Like *D. exannulatus* and *D. fluitans*, it does not occur in the central part of North America. *D. revolvens*, of the boreal-montane species, is the most restricted in range and variability. Although it seems a well-defined and natural species to me, many bryologists have recognized a variety, and even another species, *intermedius*. It is definitely restricted in its habitat to boreal bogs and swamps and arctic meadows, and therefore has a more northern distribution than any other boreal-montane species.

Because *D. uncinatus* grows in xerophytic or mesophytic instead of hydrophytic habitats, conditions governing its distribution and variability are different from those affecting other species of *Drepanocladus*. Like *D. revolvens*, it is a well-defined, natural species. In fact, it is so distinctive in its habitat and diagnostic features that Loeske (1907) created the genus *Sanionia* for *D. uncinatus* and its varieties. Nevertheless, it is much more variable and adaptable than any of the arctic-alpine species and it has the distribution characteristic of the boreal-montane species of *Drepanocladus*.

Vascular plants with similar distribution.—It is interesting to compare the ranges of bryophytes with those of vascular plants. The following lists, which include only a few of the possible examples, were compiled from Hultén (1937) and Polunin (1940); the nomenclature follows Polunin.

Although the range of any single species cited here may be discontinuous, together they show a distribution similar to that of the arctic-alpine species of *Drepanocladus*.

Antennaria angustata Greene
Arctagrostis latifolia (R. Br.) Griseb.
Carex rariflora (Wahlenb.) Sm.
Cochlearia officinalis L.
Colpodium fulvum (Trin.) Griseb.
Draba alpina L.
Draba cinerea Adams
Draba nivalis Liljebl.
Dryopteris fragrans (L.) Schott.
Elymus arenarius L.
Luzula nivalis (Laest.) Buerl.

Lychnis furcata (Raf.) Fernald
Pedicularis labradorica Wirsing
Pedicularis lapponica L.
Pedicularis sudetica Willd.
Poa glauca M. Vahl
Primula egalikensis Wormskj.
Puccinellia phryganodes (Trin.) Scribn.
Ranunculus nivalis L.
Salix arctica Pall.
Stellaria humifusa Rottb.

The following plants have ranges similar to the boreal-montane species of *Drepanocladus*.

Alopecurus alpinus Sm.
Andromeda Polifolia L.
Artemisia borealis Pall.
Astragalus eucosmus Robinson
Callitriche verna L.
Carex Bigelowii Torrey & Schwein.
Carex bipartita All.
Carex capillaris L.
Carex misandra R. Br.
Carex rupestris All.

Lychnis apetala L.
Oxyria digyna (L.) Hill
Oxytropis foliolosa Hook.
Pedicularis capitata Adams
Pedicularis lanata Cham. & Schl.
Poa alpina L.
Poa arctica R. Br.
Polygonum viviparum L.
Potentilla nivea L.
Potentilla palustris (L.) Scop.

<i>Cassiope tetragona</i> (L.) D. Don.	<i>Primula stricta</i> Hornem.
<i>Draba fladnizensis</i> Wulfen	<i>Pyrola secunda</i> L.
<i>Dryas octopetala</i> L.	<i>Ranunculus pedatifidus</i> J. E. Smith
<i>Empetrum nigrum</i> L.	<i>Ranunculus pygmaeus</i> Wahlenb.
<i>Epilobium angustifolium</i> L.	<i>Ranunculus sulphureus</i> Solander
<i>Eriophorum Scheuchzeri</i> Hoppe	<i>Saxifraga caespitosa</i> L.
<i>Festuca brachyphylla</i> Schultes	<i>Saxifraga cernua</i> L.
<i>Hippuris vulgaris</i> L.	<i>Saxifraga flagellaris</i> Willd.
<i>Juncus albescens</i> (Lange) Fernald	<i>Saxifraga hieracifolia</i> Waldst. & Kit.
<i>Juncus biglumis</i> L.	<i>Saxifraga oppositifolia</i> L.
<i>Juncus castaneus</i> Smith	<i>Silene acaulis</i> L.
<i>Kobresia simpliciuscula</i>	<i>Thalictrum alpinum</i> L.
(Wahlenb.) Mack.	<i>Tofieldia palustris</i> Wahlenb.
<i>Koenigia islandica</i> L.	<i>Vaccinium Vitis-Idaea</i> L.
<i>Ledum palustre</i> L.	<i>Veronica alpina</i> L.
<i>Luzula spicata</i> (L.) DC.	<i>Woodsia ilvensis</i> (L.) R. Br.

Drepanocladus and Pleistocene Glaciation

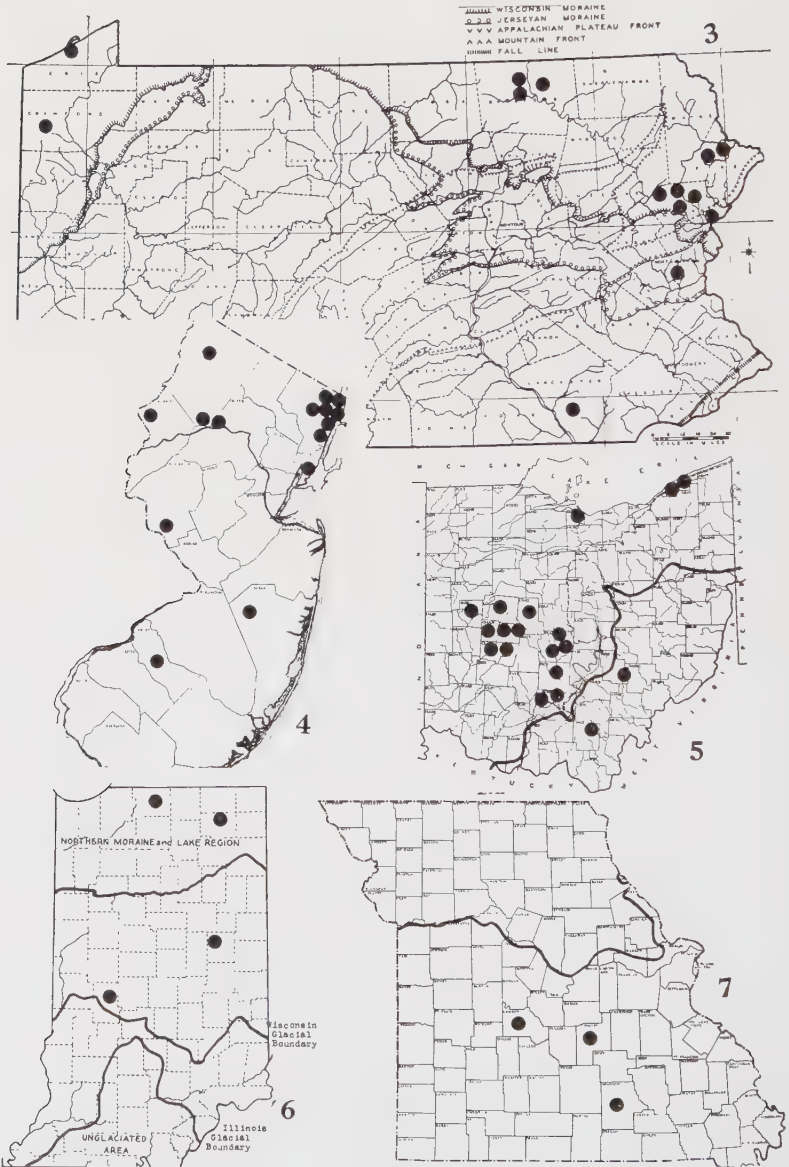
Correlation of present distribution of Drepanocladus with the Pleistocene glaciation.—The present range of *Drepanocladus* coincides rather well with the maximum extent of continental glaciation during the Pleistocene epoch. This is especially well shown by the correlation of the southernmost boundary of the distribution of the genus and the boundaries of the various Pleistocene till sheets. Since I have considered only American species, I shall confine specific examples of distribution to North America.

Eastern North America.—In the eastern part of North America, the genus is not found in states (with the exception of West Virginia) that lie entirely south of the maximum extent of the Pleistocene glaciation. For instance, there are no records of *Drepanocladus* in Virginia, Kentucky, or Arkansas or in the states southward. However, *Drepanocladus* shows a significant distribution in the states which were partially glaciated. In Pennsylvania, Indiana, Ohio, and New Jersey, the genus occurs commonly only in the glaciated area of the state, although there are isolated stations south of the maximum extent of the glaciation as it is recognized today (see maps 3 to 6).

The only plants of *Drepanocladus* I have seen from regions south of the Wisconsin and Jerseyan moraines in Pennsylvania are J. K. Small's collections of *D. fluitans* from Smithville Swamp, Lancaster County (map 3). Dr. John M. Fogg of the University of Pennsylvania says (*in litt.*):

Smithville . . . has long been recognized as one of the most peculiar spots in the south-eastern corner of the state. It is, or was, at one time, a large bog, or rather a series of bogs, in which occurred a remarkable assemblage of coastal plain species, among which were intermixed a few plants of distinctly boreal range. Among the latter the most spectacular was *Juncus balticus* var. *littoralis*, here known at its only station, I believe, south of the Wisconsin moraine. Unfortunately, the Smithville area has been almost entirely destroyed by subsequent draining and filling, so that there is little, if anything, of real botanical interest there today.

In New Jersey, *Drepanocladus* is abundant in the glaciated parts of the state; I have seen numerous collections from the heavily glaciated Sussex, Morris, Warren, Bergen, and Hudson Counties. The genus also occurs in



The distribution of *Drepanocladus* in relation to the glacial border. Map 4, In Pennsylvania. Map 4, In New Jersey. Copyright, American Map Co., Inc., New York, No. 10589. Map 5, In Ohio. Reproduced through courtesy of C. H. Jones. Map 6, In Indiana. Reproduced through courtesy of Charles C. Deam. Map 7, In Missouri. Copyright, American Map Co., Inc. New York, No. 10589.

New Jersey in the pine barrens of Ocean and Burlington Counties, a region where numerous swales, sloughs, and intermittent streams provide suitable habitats (map 4).

Ohio has long been noted for the diverse geographic affinities of its flora because of its numerous disjunct species characteristic of prairie, plains, hemlock-hardwood, and boreal plant formations. The persistence of boreal relic species in bogs, coves, on cliff tops, and sand dunes is a conspicuous feature of the glaciated area of the state. A few of these boreal relics are found in the unglaciated area of Ohio. According to Braun (1928), groves of *Thuja occidentalis* L. occur along the borders of the Illinoian drift at the edge of the "hill country" where the varied topography favors the persistence of diverse plant communities. Associated with arbor vitae are *Carex eburnea* Boott. and *Viola arenaria* DC.

Other northern plants which occur in the glaciated area of Ohio or along the borders of the Illinoian drift are (Thompson 1939): *Alnus americana* L., *Betula pumila* L., *Epipactis tessellata* (Lodd.) A. A. Eaton, *Hypericum majus* (Gray) Britton, *Larix laricina* (DuRoi) Koch., *Lathyrus palustris* L., *Ledum groenlandicum* Oeder., *Linnaea americana* L., *Menyanthes trifoliata* L., *Potentilla palustris* (L.) Scop., *Pyrola secunda* L., *Salix candida* Flugge, *Salix pedicellaris* Pursh., *Shepherdia canadensis* (L.) Nutt.

Two relic localities for *Drepanocladus* are known in Jackson and Perry Counties (map 5). Of these areas Dr. R. T. Wareham of Ohio State University says (*in litt.*):

Liberty Township, Jackson County is perhaps the richest area floristically of any in Ohio. There are high cliffs, deep gorges, and many springs. Proglacial Lake Tight (Wolfe 1942) covered a large portion of the county but perhaps only half of Liberty Township. Perry County has had much the same history but the cap rock is somewhat different and therefore the topography is different.

Braun (1928) believes that the boreal colonies of the unglaciated area of Ohio are probably relics of the coniferous belt established during the Illinoian glaciation and persist today for the most part in areas not especially favorable to the deciduous forest. Since they occur on areas which, to our knowledge, have never been glaciated, they probably existed in their present localities during most of the Pleistocene or at least since the Illinoian.

Drepanocladus has never been collected on the unglaciated portion of Indiana nor on the Illinoian till sheet in that state (map 6). Flowering plants that show a similar distribution in Indiana (Welch 1936) are: *Carex projecta* Mack., *Circaea alpina* L., *Cornus rugosa* Lam., *Cypripedium reginae* Ait., *Diervilla lonicera* Mill., *Gentiana procera* Holm., *Habenaria orbiculata* (Pursh) Torr., *Hydrocotyle americana* L., *Maianthemum canadense* Desf., *Pinus strobus* L., *Potentilla fruticosa* L., *Prunus nigra* Ait., *Schizachne purpurascens* (Torr.) Swallen, *Taxus canadensis* Marsh, *Vaccinium canadense* Kalm.

Drepanocladus occurs in Missouri in the Ozarks south of the Kansan and Iowan till sheets (map 7). *D. aduncus* has been collected in Ellis Spring, Camden County and in springs near Round Spring State Park, Shannon

County. Since the genus apparently occurs only in the springs in Missouri, Steyermark's study of the phanerogamic flora of the fresh-water springs in the Ozarks (1941) is pertinent. He has reported that several phanerogams which are otherwise restricted to glaciated areas in North America occur in the springs in the Ozarks, namely: *Anacharis occidentalis* (Pursh) Victorin, *Eleocharis acicularis* (L.) R. & S., *Lemna trisulca* L., and *Veronica connata* Raf. These plants, which also occur in Iowa, Minnesota, Wisconsin, Indiana, and states northward, do not occur in northern Missouri but are restricted to the Ozarks. Steyermark believes that the limiting factor is the

suitable habitat of cooler waters found in the Ozark springs as compared to the temperature found in rivers, lakes, sloughs, and other types of aquatic environment in other parts of the state. . . . The only property possessed by Ozark Springs which is not duplicated in streams, lakes, sloughs, and other bodies of water in Missouri, is cold water . . . species may be found abundantly in spring water, but are totally lacking in the slightly warmer but otherwise similar waters of the Ozark streams into which the spring water empties. . . . Sometimes the cooler spring water persists for a few hundred feet down the main stream into which it empties, and as long as the influence of the cooler temperature of its water persists, so does the vegetation characteristic of the spring water (p. 530).

Steyermark believes that these plants characteristic of springs in the Ozarks do not occur in the northern glaciated area of Missouri because there are no suitable habitats on the Kansan and Iowan till sheets of that region. Missouri was not covered by the more recent Illinoian and Wisconsin ice sheets; therefore the morainal topography of northern Missouri is old and is not characteristic of areas which have been glaciated. Consequently, no habitats suitable for *Drepanocladus* exist in that region.

West Virginia is the only state entirely unglaciated during the Pleistocene from which I have seen specimens of *Drepanocladus*. The occurrence of the genus in West Virginia is apparently due to drainage and soil factors combined with a relic Pleistocene distribution. Core (1932) discusses the effect of the Pleistocene glaciation upon the flora of West Virginia as follows:

The Pleistocene glaciation did not reach West Virginia, the terminal moraine being 25 miles or more from the northern boundaries, yet it is probable that at that time at least the northern part of the state must have presented the aspect of an Arctic tundra, while many Canadian species were forced hundreds of miles farther south. Upon the retreat of the ice sheet and the consequent northward migration of biota, some of these species were left behind on the cold mountain tops throughout the Appalachians. Relic colonies of tundra, persisting in mountain glades, were surrounded by the migrating forests and are still in process of being replaced by succession (p. 70).

A combination of factors has enabled these northern habitats to persist in the mountains of West Virginia today. Core states:

Here and there throughout the higher mountains, where the drainage is impeded due to resistant masses of conglomerate or other sandstone, are formed topographic features known locally as "glades," which resemble in a striking manner the bogs of farther north. In these glades may be found species of *Sphagnum*, *Cladonia*, etc., as well as such vascular plants as *Aspidium simulatum*, *Larix laricina*, *Carex trisperma*, *Pogonia ophioglossoides*, *Calopogon pulchellum*, *Alnus incana*, *Coptis trifolia*, *Drosera rotundifolia*, *Geum rivale*, *Vaccinium oxycoccos* . . . (p. 68).

I have seen two specimens of *D. fluitans* and one of *D. exannulatus* var. *Rotae* from Pocahontas County. Dr. Core says of this area (*in litt.*):

There are, indeed, many plants of unequal distribution in the Pocahontas County area. . . . Northern species of vascular plants ranging southwards along the high Alleghenies of Pocahontas and (or) adjacent counties include *Picea rubra*, *Betula lutea*, *Sorbus americana*, *Acer spicatum*, *Clintonia borealis*, *Streptopus roseus*, *Cornus canadensis*, *Chiogenes hispidula*, *Potentilla tridentata*, *Pogonia ophioglossiodes*, *Coptis trifolia*, *Andromeda glaucophylla*, *Geum rivale*, *Vaccinium macrocarpon*, and *Menyanthes trifoliata*.

The only other locality in West Virginia from which I have seen plants of *Drepanocladus* (*D. fluitans*) is the Cranesville Swamp in Preston County. Dr. Core says of this area (*in litt.*):

Cranesville Glade is a local name for a large swamp 12 miles north of Terra Alta, in Preston County. The area, covering several hundred acres, lies at an elevation of approximately 2600 feet and is surrounded by low mountain ranges that rise gradually to over 3000 feet. The swamp was originally heavily wooded with tamarack (southernmost station), red pine (until recently southernmost known station), black ash, spruce, etc., with open places where grow *Sphagnum*, cranberry, thread-of-gold, *Dalibarda*, etc. It is, thus, distinctly a northern habitat.

Western North America.—Extensive mountain glaciation in western North America was concomitant with the continental glaciation of the eastern part of the continent. In both regions apparently several glacial stages were separated by interglacial stages of various lengths. Times when many of the deep canyons were occupied by long tongues of ice alternated with interglacial periods when such glaciers shrank to mere vestiges or entirely disappeared. Blackwelder (1931) has proposed a tentative correlation of glacial stages in western United States (as known in Montana, Wyoming, Colorado, Utah, Nevada, and California) with the well known Wisconsin, Iowan, Illinoian, Kansan, and Nebraskan stages in eastern United States. He believes that the best evidence for this general correlation is the "climatic pulsations for which the Pleistocene period is noted. Such climatic variations, if due to general atmospheric or perhaps astronomic causes must have affected all parts of the region." Ray (1940) has shown further that the five sub-stages of the Wisconsin glaciation are the same in the Cache la Poudre Valley in the Colorado Front Range as in the Southern Rocky Mountains from southern Wyoming to Santa Fe, New Mexico. Furthermore, Bryan (1941) has correlated stages in the southern Rockies with the continental glaciation of North America and Europe.

It seems logical that, since the glacial history in eastern and western North America was similar, it should have produced similar effects on vegetation. The cordilleran glaciation, as well as the continental glaciation, formed many bogs and swamps which now provide suitable habitats for *Drepanocladus*. Consequently, the distribution of the genus today parallels the maximum extent of cordilleran, as well as continental, glaciation during the Pleistocene; a map showing the extent of glaciation in western North America very much resembles a distribution map of *Drepanocladus* in that region.

A detailed study of the distribution of *Drepanocladus* in the western United States shows that the southern limits of the genus are always in the

mountains. *D. aduncus* is found in Nebraska in the Pine Ridge; in New Mexico in the Gallina Mountains and in the Sangré de Cristo Range; in Utah in the mountains north of Great Salt Lake and the Uinta Mountains; and in California in the San Bernardino Mountains. The southern limits of *D. exannulatus* are in the Tetons of Wyoming; the Rocky Mountains of Colorado; the canyons of Tavaputs Plateau in Utah; the Sierras of California. *D. fluitans* occurs as far south as the Absaroka range in Wyoming and the Rockies in Colorado.

The same factors that limit *Drepanocladus* to the mountains in the western United States account for its occurrence in the mountains of Mexico, Guatemala (*D. exannulatus* and *D. aduncus*) and in the Chilean Andes (*D. uncinatus*). It is apparently less common in the southern cordilleran ranges than in the northern mountains.

The ability of Drepanocladus to pioneer on glaciated areas.—The wide distribution of *Drepanocladus* over the glaciated areas of the world is directly related to its remarkable ability to pioneer on new lands. The several retrogressions of the ice front during the Pleistocene with each resulting interglacial period opened vast areas for plant colonization. That the species of *Drepanocladus* established themselves during the interglacial periods in areas previously covered by ice is proven by the numerous fossil mosses found in interglacial deposits.

A large number of fossil *Drepanocladi* have been found in Iowa. I have seen the following collections: *D. exannulatus*, 15 feet below the surface near Mud Lake, Emmett County, B. O. Wolden (NY, DUKE) (Grout, 1930, as *D. fluitans* var. *Jeanbernati*); *D. revolvens* and *D. fluitans*, 32 feet below the surface, Oelwein, Fayette County, T. H. Macbride (NY) (Holzinger, 1903; Savage, 1905; Macbride, 1897).

Steere (1942) has studied some fossil material from Afton, Union County, Iowa. Included among other Bryophyta were several species of *Drepanocladus*: *D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. revolvens*, and *D. apiculatus*, a fossil species closely related to *D. revolvens*. These mosses were deposited during the first interglacial period, the Aftonian, between the Nebraskan and Kansan invasions.

There are numerous other references in the literature to species of *Drepanocladus* found in Aftonian deposits in Iowa: *D. fluitans* from Dodge Township, Union County (Savage, 1904); *D. fluitans* var. *glaciale* from Iowa City, Johnson County (Holzinger, 1903); *D. aduncus* from Davenport, Scott County (Pratt, 1876).

Records of fossil *Drepanocladi* are not confined to Iowa, however. I have seen peat from Madoc County, California, composed entirely of *D. aduncus* var. *typicus* (aquatic phase) which must occur in large quantity, as it is a commercial product. R. S. Williams (1930) has reported three fossil mosses from Minneapolis, Minnesota, including the new fossil species, *D. minnesotensis* which is closely related to, if not identical with, *D. aduncus*. Cooper and Foot (1932) in discussing the same deposit, mention also "*D. fluitans submersus*."

The most striking feature about these interglacial fossils is that all the species represented are boreal-montane species. This fact leads one to conclude that the boreal-montane species of *Drepanocladus* were colonizing on the Kansan till sheet during the Aftonian interglacial period just as they are colonizing on the Wisconsin till sheet today. The fact that none of the arctic-alpine species are found south of the arctic, either as living or fossil plants, points to the conclusion that they have always been confined to the extreme north.

Survival of Drepanocladus during the Pleistocene.—Since the species of *Drepanocladus* are now confined to the part of the world glaciated during the Pleistocene, it is obvious that glaciation is an important limiting factor in distribution. Because *Drepanocladus* grows only in the bogs and swamps that are the result of glaciation, the thought that its present distribution is merely the result of a habitat preference immediately arises. However, several facts indicate that the situation is more complex. One species, *D. uncinatus*, is almost xerophytic, growing over logs, banks, and the bases of trees. These habitats are not confined to areas which have been glaciated, yet *D. uncinatus* is. Furthermore, certain species of *Leptodictyum*, *Hygroamblystegium*, and *Cratoneuron* are frequently found growing with *Drepanocladus*. These species also occur in the swamps of Florida and other semi-tropical regions where *Drepanocladus* has never been found. The difference, then, is one of plants and not of habitats.

Before considering the mechanism whereby the Pleistocene glaciation might have affected the genus, it is important to consider the survival of *Drepanocladus* during the time when much of its present area was ice covered.

There are four types of places in which *Drepanocladus* might have found refuge during the Pleistocene: areas outside the maximum boundaries of the ice sheets, such as (a) south of the Pleistocene ice (b) north of the ice sheets (c) on unglaciated lowlands, and areas within the generally glaciated territory, such as nunataks.

Survival outside the maximum boundaries of the ice sheets.—*a. South of glaciation.* We have no reasons, from either fossil or modern evidence, to believe that plants were absent close to the edge of the ice. Studies of modern glaciers and Pleistocene fossil deposits indicate the conditions at the edge of the continental glaciers.

Greenland, which, except for a narrow coastal margin and the northern regions, is today entirely covered with an ice cap, affords the best example of the continental Pleistocene glaciers. Greenland has been rather well explored and the vegetation at the ice front is well known. Koch (1928) describes one of the smaller ice sheets as follows:

The ice front . . . consists of a series of snow-drifts whose length varies from 50-800 meters. . . . After crossing the snow-drifts we encountered a morainic landscape. . . . Hills, 5-10 meters high alternated with sandy plains and depressions filled with clay and occasional small lakes and snow-drifts occurred. Patches with vegetation also occurred, for instance, *Papavers*, *Cerastium*, *Koenigia*, *Saxifraga*, *Luzula*, *Carex*, as also moss and lichens . . . (p. 226).

Swamps result from the melting of the ice. Seidenfaden (1931) states:

In places where the water has no outlet, thus in all depressions in the ground, there will be a surplus of water as soon as the melting of the snow has set in. . . . In such places there will, according to circumstances, be formed a swamp or a lake with its own more or less varying types of vegetation. . . . These swamps, the only formation in which mosses play an essential part, occur everywhere where there is the slightest depression in the ground; it must be remembered that the solid substratum (ice) lies immediately below the surface of the land and at a nearly constant distance from it; thus the presence of a ridge only about 80 cm. high will give rise to the formation of a swamp behind it (p. 7).

According to Koch (1928) the vegetation on the north coast of Greenland is restricted to such "places where water has gathered owing to the form of the ground. This is particularly below the edges of glaciers and of large snow drifts, from which water trickles and round the shores of small lakes" (p. 366). Thus it is obvious that not only are there suitable habitats for such bog and swamp plants as *Drepanocladus* near glaciers, but also that those plants are actually living in such habitats today.

Wilson (1932) in his study of the fossil remains in the Two Creeks Forest Bed, has been able to reconstruct conditions as they probably existed at the edge of the Pleistocene ice. The Two Creeks forest in Manitowac County, Wisconsin, existed during the interglacial interval between the late and middle substages of the Wisconsin glaciation. Fossil logs show that the interglacial interval must have been long enough to allow the growth of an 82 year old forest. From the condition of the stumps, Wilson concluded that the trees were living when the glacier buried them.

All the logs . . . show ragged splintering ends in consequence of glacial action upon the trees. This condition indicates a violent twisting and bending of live trees before they were felled (p. 37).

Some of the leaves of the fossilized mosses contained remnants of chloroplasts which Wilson interprets as "strong evidence that the mosses were living at the time of burial."

That plants were living when the ice readvanced indicates that there was not a large barren area immediately before the ice, and that plants could remain alive at the ice front. Study of the Two Creeks Forest Bed also proves that bogs appeared south of the advancing ice supplanting the mesophytic conditions which previously existed. The land snails, the mosses (e.g. *Bryum cyclophyllum* (Schw.) B. & S.), and the grasses characteristic of a forest floor vegetation, as well as the poorly developed (sometimes wanting) peat indicated to Wilson that the Two Creeks Forest Bed was, at one stage of its existence, a mesophytic forest. From the remains of this forest there is a gradual transition to entirely aquatic species of plants and animals. Wilson states (p. 41) that apparently the only plants that were able to thrive during the last years of this interval were aquatic and subaquatic mosses including *Byrum bimum* Schreb., *Calliargon cordifolium* Kindb., *C. turgescens* (Jens.) Kindb., *Campothecium nitens* Schlp., *Campylium stellatum* (Schreb.) Bryhn, *Drepanocladus aduncus* Mönkem. var. *pseudofluitans* Sanio, *D. revolvens* (Sw.) Warnst., *D. Sendtneri* (Schp.) Warnst., *D. vernicosus* (Limpr.) Warnst.,

D. Wilsoni (Schp.) Roth, *Scorpidium scorpioides* (L.) Limpr. Mollusks found at the same level as the above named mosses were the following aquatic species: *Gyraulus circumstriatus* (Tryon), *Fossaria parva* (Lea.), *Pisidium* sp.

That the character of the forest changed several times during its history is shown by the three distinct periods apparent in the fossil remains: (1) aquatic and semi-aquatic mollusks on top of the varved clay of early Lake Chicago; (2) moist- to dry-woodland mosses, mollusks, mites, fungi, and trees marking an interval of dry land; (3) water mosses, water mollusks, and sediment caused by the re-advance of the ice blocking the drainage.

Cooper and Foot (1932), by comparing the fossil record of a late-Pleistocene community in Minneapolis, Minnesota, with bogs existing today in Alaska, have been able to add to our knowledge of conditions at the edge of the Pleistocene ice sheets. Of the fossil bed in Minneapolis they say:

The history recorded in this bed is as follows. Sedimentation, which had been heavy for a time, gradually slackened and aquatic mosses began to grow, *Drepanocladus*, having a hard time of it at first, finally attaining dominance. Control passed from one to another of the mosses [*Neocalliergon integrifolium* Williams and *Calliergon giganteum* (Schp.) Kindb.], until the renewal of active sedimentation put an end to their growth. The natural supposition would be that the mosses floated just below the surface of the pond . . . (p. 67).

The mollusca, pollen, cones, and fruits enable the authors to reconstruct the vegetation of the time as follows:

A morainic or outwash pond, sometimes flooded by silt-laden water, supported an intermittent vegetation of mosses, *Chara* and pondweeds, to which, if it were worth while, we might add an extensive group of probable companion species. . . . Nearby, in depressions of less depth, or possibly in sheltered re-entrants of this low area, grew communities of bog trees with their characteristic accompanying species. Upon the uplands . . . stood the climax forest of white spruce, balsam fir, white pine and birch, just as we find it today in northernmost Minnesota and upon Isle Royale. Branches, twigs, cones, and seed may have fallen from these trees directly into the water, and quantities of their pollen would inevitably reach the same destination.

During an expedition to southeastern Alaska in the summer of 1929 Cooper studied a locality that is remarkably parallel to the one in Minneapolis—a morainic pond in front of the Davidson Glacier.

The pond in question lies near the outer margin of the morainic belt, and is surrounded by a dense forest of youthful Sitka spruce (*Picea sitchensis* Carr), in height seventy or eighty feet, with a maximum diameter of two feet. A few cottonwoods (*Populus trichocarpa* Hook.) are interspersed.

By studying the ages of the trees (60-76 years), and with knowledge of similar localities in southeastern Alaska, Cooper concluded that "the spot was uncovered by the melting of the ice one hundred to one hundred and fifty years ago." He continues:

The open water of the pond contained quantities of one of the same mosses found in the Minneapolis locality—*Calliergon giganteum*—also enormous amounts of *Chara* and two species of *Potamogeton*. In addition, another aquatic moss was present—*Fontinalis antipyretica gigantea* Sull. Emergent aquatics filled the shallower portions, *Equisetum fluviatile* L. being most important.

Therefore, from the fossil and living evidence, it is obvious that plants (including *Drepanocladus*) lived in favorable habitats at the edge of the

Pleistocene ice sheets. That habitats favorable for *Drepanocladus* commonly existed at the edge of the ice is proven by the swamps and lakes formed at the edge of the modern glaciers in Greenland and Alaska and by the fossil interglacial bogs. Moreover, if ice-buried Greenland can support along its narrow rim today over four hundred species of vascular plants and numerous cryptogams, certainly plants could have existed along the edge of the Wisconsin ice. It is equally obvious that the plants living at the edge of the ice could invade territory immediately after the melting of the ice sheets. If it took less than 150 years for bryophytes to come into the morainic ponds at the Davidson Glacier in Alaska, it should have taken no longer in the Pleistocene. Moreover, the fossils prove conclusively that the glaciated area was reinhabited with plants during each interglacial period.

In studying present ranges of the species of *Drepanocladus*, it is obvious that only the boreal-montane species, and not the arctic-alpine species, could and did exist south of the Pleistocene ice. All the boreal-montane species (except *D. vernicosus* and *D. uncinatus*) have been found in interglacial deposits; the two fossil species (*D. minnesotensis* and *D. apiculatus*) are closely related to the living boreal-montane species *D. aduncus* and *D. revolvens*. The presence of the boreal-montane species in the fossil beds of Iowa near the southern limit of their range proves that those species existed there during interglacial times and indicates that when Iowa was ice-covered, *Drepanocladus* probably lived in the ponds and lakes at the ice-front. All the locations that are today south of the maximum extent of Pleistocene glaciation, such as: the pine barrens of New Jersey; Lancaster County, Pennsylvania; Jackson and Perry Counties, Ohio; the Ozarks of Missouri; and Preston and Pocahontas Counties of West Virginia may be relics of this Pleistocene distribution. The fact that the boreal-montane species today extend to and slightly beyond the southern boundary of the continental glaciation is an indication that they lived there during the Pleistocene epoch.

The retreat of the ice front opened many avenues for the northward migration of plants and recolonization took place along the coastal plain as well as in the interior of the continent. During the maximum development of the last ice advance (and probably during the entire Pleistocene), a very large portion of the now submerged coastal bench was above the sea level, opening a route to the north. There are many flowering plants whose present distribution can best be explained by the presence of a coastal plain along which migration could take place.

Fernald (1911) explained the occurrence of a large percentage of coastal plain species in Newfoundland by means of the same coastal plain along which plants could have migrated:

Here, then, would be a strip of sands and similar soils stretching with only slight interruptions from our South Atlantic coast to Newfoundland, and it is probable that not far in the wake of the receding ice and the more boreal plants and animals the Coastal Plain plants with the Newfoundland vole and the muskrat crossed on this sandy bridge to Newfoundland. . . .

Potter (1932) was interested in such plants as *Zannichellia palustris* L. var. *major* (Boenn.) Koch., *Glaux maritima* L. var. *obtusifolia* Fernald, *Caex mari-*

tima O. F. Mueller, *Juncus Gerardi* Loisel., *Plantago juncooides* Lam. var. *decipiens* (Barneoud) Fernald, and *Zosteria marina* L., which are distributed along the Atlantic coast from New Jersey to the Gulf of St. Lawrence and also occur in the Hudson Bay region. Potter explains the distribution of these plants by postulating migration northward along the Atlantic coastal plain and then to the Hudson Bay along the shores of inland post-Pleistocene seas.

The central part of the continent could have been reached, as Gleason (1922) has shown, not only by migration directly northward, but also by migration along the shores of the Champlain Sea. During the Algonquin and Nipissing stages of the Great Lakes entrance to the lake region was gained along the Kirkfield and North Bay outlets. The occurrence in the Great Lakes region of such coastal plain species as *Ammophila arenaria* (L.) Link., *Elymus arenarius* L., *Juncus balticus* Willd., *Cakile edentula* (Bigel.) Hook., *Prunus pumila* L., *Lathyrus maritimus* (L.) Bigel., *Hudsonia tomentosa* Mitt., and *Tanacetum huronense* Nutt. have been explained by Gleason by means of such a migration route.

Although these various migration routes have been most frequently used to explain disjunct distributions among coastal plain species, there is no reason to suppose that other plants, such as *Drepanocladus*, which survived south of the glaciation, did not use the same routes to attain their present widespread boreal distribution. The boggy meadows and shallow pools which formed after the retreat of the ice would have provided especially favorable habitats for the migration of *Drepanocladus*.

b. Survival north of glaciation.—Although relatively little study has been made of the northern border of the continental ice sheets, the general consensus of opinion among geologists is that large parts of northern Alaska and the arctic archipelago were not glaciated during the Pleistocene.

Simmons (1913) states that "the northern [border] seems to have coincided rather closely with the present continental shoreline, with the exception of Boothia Felix and the Melville Peninsula" (p. 153). He discusses the glaciation in the arctic archipelago further as follows:

The only part of the Arctic Archipelago that shows signs of a considerable former glaciation is southern Baffin Land. . . . The glaciation of [the arctic archipelago] never reached to form large icesheets or continuous inlandices, only isolated glaciers in the valleys and thin icecaps over the summits of some mountains.

Of Alaska, Chamberlain and Salisbury (1907) say:

. . . mountain glaciation was strongly developed on the ranges adjacent to the Pacific, particularly on the side next to the ocean. On the north side, the ice pushed well out from the high mountains but did not reach the Yukon . . . the plains of Alaska seem to have been free from glaciation even at the stages when the waters of the Ohio and Missouri were being turned from their courses by the encroaching ice sheets 2000 miles farther south.

Not only was the arctic archipelago partly unglaciated during the Pleistocene, but also it was uplifted to form a land continuous with the North American continent. Therefore, there was considerable area north of the continental glacier where plants might have lived during the Pleistocene.

Fernald (1925) was the first to correlate the driftless condition of the arctic archipelago with the fact that plants persisted there during the Pleistocene epoch.

The Arctic Archipelago during Pleistocene time was uplifted and formed continuous land confluent with the present North American continent; and the consensus of geological opinion is, that it was outside of the area covered by the great glacial fields of North America. Then, as now, it was a region with only local valley-glaciers. Alaska, too, has had only local glaciers and these chiefly at the southern border, where warm and moist winds have favored abundant precipitation. . . . The plants of the Arctic Archipelago . . . are considered, then, to have lived throughout Pleistocene time in the Arctic.

The arid northwestern area of Greenland probably has a climate today similar to that of the arctic archipelago during the Pleistocene. However, that plants exist today in north Greenland, while the rest of the island is ice-covered indicates that plants could have lived in arctic America while that continent was covered with continental glaciers.

When we realize that most of the known modern species of *Drepanocladus*, including all the arctic-alpine species have been found in the partly unglaciated arctic archipelago, it is reasonable to suppose that they inhabited that territory before and during the Pleistocene. The main difference in distribution, both Pleistocene and modern, between the arctic-alpine and boreal-montane species lies in the fact that the latter group also extends far enough southward to persist at the southern border of glaciation. The arctic-alpine species, *D. badius*, *D. brevifolius*, *D. lycopodioides*, and *D. fluitans* var. *Berggreni*, as well as the boreal-montane species, *D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. revolvens*, *D. vernicosus*, and *D. uncinatus* could have survived in the bogs on the northern border of the ice. On the contrary, only the boreal-montane species could have lived in the ponds and swamps at the southern edge of the ice sheets.

As the land was gradually exposed by the melting of the Pleistocene ice, numerous migration routes to the south were opened. The ice probably lingered longest in the central part of the continent, so that the first migration southward was probably along the east and west coasts. This migration along either side of Hudson Bay would form Marie-Victorin's (1938) "rainbow" (p. 547). The boreal-montane species could have migrated along the arms of this rainbow before the routes directly south were opened. The arctic-alpine species never migrated south from their northern refuge.

c. *Survival on unglaciated lowlands.*—Plants may have survived on an unglaciated coastal plain during the Pleistocene. Although there is little geological evidence either to prove or disprove the existence of such a coastal plain, botanical evidence is so convincing that geologists have accepted it as evidence of a continuous coastal plain during the Pleistocene.

The present sea level is so high that the physical evidence as to conditions along the coast during the Pleistocene has been drowned. By studying the submarine physiography, and calculating the sea level during the Pleistocene, geologists have postulated the extent of this coastal plain. It has been estimated

that with the lowering of the sea level 125 feet, a coastal plain 150 miles wide would have been formed. Johnson (1925) after studying the Gulf of Maine says:

The submarine physiography demonstrates the presence of a normal, maturely dissected coastal plain bordering the New England-Acadian oldland at a period which would account for the very early migration of the Pine Barren flora [to Newfoundland] . . . instead of a temporary land bridge due to bulging at the margin of the glacier, there was a long-enduring coastal plain topography extending continuously from New Jersey and southward to beyond Newfoundland.

Fernald (1911) in his analysis of the flora of Newfoundland, provided the first and the best botanical evidence of a continuous coastal plain during the Pleistocene. He points out that 118 species of plants belonging to the pine barren and coastal plain floras of New Jersey and the south are known from remote outlying stations along the coastal strip of New England and the Maritime Provinces and that over 7% of the plants of Newfoundland are coastal plain species. Fernald, to explain the similarity of the Newfoundland flora and fauna to that of the Atlantic area of Europe, postulates a migration of biota across the mid-Tertiary land and a subsequent isolation along the northeastern coast of North America. This implies "some tract along the coast, especially of Acadia, and Newfoundland, which held this flora and fauna continuously through the Pleistocene. . ."

That *Drepanocladus* can live in such coastal plain habitats is proved by its occurrence today on the coastal plain of New Jersey and on the plains around the Great Lakes. It seems extremely probable that the boreal-montane species of the genus lived on this coastal plain that is thought to have existed during the entire Pleistocene. The same migration routes that were available to the plants surviving south of the ice sheets would have been opened by the receding ice to these plants on the coastal plain.

Survival within generally glaciated areas.—Fernald, with his Nunatak hypothesis was the first to propose that arctic-alpine plants might have persisted on ice-free lands in the arctic and upon small unglaciated areas (Greenland-Eskimo, "nunataks") either within or near the margins of the ice fields.

Fernald studied the alpine tablelands and ravines of the Shickshock Mountains of the Gaspé Peninsula and the Long Range of western Newfoundland and found growing with the characteristic arctic-alpine plants many species which were absent farther north and which were known elsewhere only in the western cordillera, Alaska, or the Altai of Siberia. He correlated this disjunct distribution with the fact that these areas were not glaciated during the Pleistocene. His hypothesis is summarized as follows:

. . . it is the conclusion of such Canadian geologists as Bell, Chalmers, Coleman, and Alcock, that the Labrador ice-sheets did not cross the Shickshock range and that in the eastern two-thirds of the Gaspé Peninsula glaciation was extremely local, many areas remaining quite free from ice. Analysis of the local distribution on the Peninsula of the Cordilleran and other western plants and of their endemic allies brings out very strikingly the fact that their stations are just exactly on the spots which escaped extreme glaciation. . . .

There has been an active controversy between geologists and botanists about the nunatak hypothesis ever since it was proposed in 1925. The hypothesis does not completely explain many of the relic areas: for instance, those at Bic, Rimouski County, Gaspé Peninsula, Quebec; on the Mingan Islands; and Anticosti. These areas have no actual nunatak areas (or only exceedingly small ones), or were covered by the post-Pleistocene invasion of the Champlain Sea. Furthermore, Flint, Demorest, and Washburn (1941) have shown that the Shickshock Mountains, the best evidence that Fernald had of nunataks, were probably covered with ice during the Pleistocene:

Detailed search failed to produce any direct evidences of glaciation through the highest 530 feet [on Tabletop Mountain]. Throughout this vertical distance evidences of any possible glaciated surfaces are obscured by mantles of locally derived falsemeers that presumably originated in post glacial time. In addition, the composition of the bed-rock is so heterogeneous that several types of erratics might be present without having been recognized. These circumstances do not demonstrate glaciation of the highest parts of Tabletop Mountain, yet there is no geologic evidence inconsistent with the view that the entire Shickshock highland was overtopped by Wisconsin ice. No geologic evidence was found suggesting that any portion of the area existed as a nunatak during the Wisconsin maximum.

After and probably also before the invasion by Labrador ice, Tabletop, at least, was a center of radial outflow from a local ice cap.

Wynne-Edwards (1939) expresses similar doubt about nunatak areas in eastern North America. He studied a region in southern Baffin Island which is still covered with ice. He found stationary ice fields on the highest ground and concluded that "it may be a fallacy to regard such centres as the Shickshocks of Gaspé as having been ice-free, because they show no evidence of ice-movement." He observed that "the first thing which happens after the retirement of an ice-cap is the almost explosive exfoliation of the surface rock" so that the presence of angular frostbroken fragments of native rock can not be used in support of the existence of nunataks. Furthermore, "Because the rock weathers so fast, many of the visible signs of glaciation are rapidly obliterated, which lends further spurious support to the nunatak theory."

Nevertheless, nunatak areas supporting a considerable flora have been found in modern glaciers. Ostenfeld (1926) has studied a small nunatak area near the north coast of Greenland. A few hardy species are able to live there under conditions which are undoubtedly as severe as those of the glacial period. From the series of nunataks, 54 species of plants were studied; of these 40 were arctic, 3 high arctic, and 11 sub-arctic and boreal.

Until Fernald's nunatak hypothesis is definitely proved or disproved, it is necessary to consider its bearing upon the distribution of *Drepanocladus*. Fernald himself was most interested in the isolated endemics and relics which might have survived on nunataks during the Pleistocene and persist there today. However, there is no reason to suppose that other plants, such as species of *Drepanocladus*, now widespread over the glaciated territory, might not also have survived on those same nunataks and have spread into adjacent territory in post-Pleistocene time.

All the boreal-montane species of *Drepanocladus* have been found on at least one of Fernald's supposedly unglaciated areas: *D. aduncus* in the Magda-

len Islands and at Bic, Rimouski County, Quebec; *D. exannulatus* on Mt. Albert and Tabletop Mountain in the Gaspé, on the Magdalen and Mingan Islands, and Anticosti; *D. fluitans* on Table Top Mt., Gaspé; *D. revolvens* on Mingan and Anticosti Islands, and Table Top Mt., *D. uncinatus* at Bic, Rimouski County, and Table Top Mt., Gaspé County, Quebec; *D. vernicosus* in the Gaspé Peninsula.

Had *Drepanocladus* survived on numerous nunataks during the Pleistocene, there would have been numerous centers from which dispersal could have taken place after the retreat of the ice.

The Effect of Pleistocene Glaciation Upon Plant Distribution

As a result of Pleistocene glaciation, two types of plant distribution are apparent in boreal regions: (1) relic, static and (2) general, widespread distribution. Whatever hypotheses are proposed to explain post-glacial dispersal of plants must take into consideration these two types of distribution.

Relic distribution.—*Bryoxiphium norvegicum* (Brid.) Mitt. and *Brothera Leana* (Sull.) C. Müll. exemplify one type of relic distribution. According to Steere (1937), wherever *Bryoxiphium* occurs it is on places which seem to have escaped at least the Wisconsin glaciation. It is found south of the maximum extent of glaciation in Kentucky, and Tennessee, comes up to the glacial border in Pennsylvania, Ohio, Indiana, and Missouri, and has been collected on Mt. Rainier, Washington, the driftless areas of Wisconsin and Minnesota, the unglaciated edge of Greenland, and southern border of Iceland. *Brothera Leana* (see Sharp 1939, p. 332 for map) shows a similar distribution: it is found in the south in Tennessee, reaches the glacial border in Pennsylvania and Ohio, and has been collected in the driftless area of Minnesota. This type of relic distribution which extends south of the maximum extent of the glaciation or centers around the driftless area of Wisconsin and Minnesota is found also among flowering plants, for example, *Talinum rugospermum* Holz., *Lespedeza leptostachya* Engelm., *Quercus ellipsoidalis* E. J. Hill.

Another type of relic distribution occurs within the generally glaciated area. Many plants which are widespread in the west occur also in isolated relic colonies in Newfoundland, eastern Canada, and northern New England. Some of the many flowering plants which have this type of relic distribution are: *Danthonia intermedia* Vasey, *Epipactis decipiens* (Hook.) Ames, *Festuca scabrella* Torr., *Habenaria unalascensis* (Spreng.) Watson, *Hordeum boreale* Scrib. & Sm., *Osmorhiza divaricata* Nutt., and *Polygonum Fowleri* Robinson. *Drepanocladus uncinatus* var. *subjulaceus* also shows this type of distribution. It is common in the west with two isolated stations in the Gaspé and Newfoundland.

General widespread distribution.—Both *Bryoxiphium norvegicum* and *Brothera Leana* represent monotypic genera and are stable and well-defined species. *Drepanocladus* and *Calliargon* contrast directly with this condition both as regards distribution and speciation. These two plastic, variable genera, with many poorly delimited species are widespread over the entire glaciated area.

Causes of these types of distribution.—Various theories have been proposed to explain why relic species such as *Bryoxiphium norvegicum* have remained so local in their distribution failing to spread into adjacent country. When Fernald felt that edaphic climatic, and other ecological factors failed to give an explanation he postulated "conservative" or "non-aggressive" species which were able to persist in territory already occupied but which were limited in their ability to pioneer. This emphasizes inherited qualities in the plant rather than external environmental features. Fernald also suggested that the conservative species were old and senescent, whereas the pioneering species were young and vigorous.

According to Fernald's thesis, then, *Bryoxiphium norvegicum* would be an old species which has passed its period of aggressiveness and is capable today of remaining in established stations, but incapable of spreading. Hence, because of its age, *Bryoxiphium norvegicum* is a stable, well-defined species.

Following this same classification, *Drepanocladus* and *Calliergon* exemplify the other extreme—they are young, aggressive, poorly defined groups. Fernald (1925) says of this type of plant:

. . . the younger arctic flora which made its way south in eastern America and Europe at least, coincidentally with the advance of the comparatively recent Labradorian or Wisconsin and the later Baltic ice sheets, has not yet had time to set off local species, though in some cases it shows minor variations which are not yet sharply differentiated; and, far from being the rarest and most retiring of relics on our mountains, these young plants, like the young of the human species, are aggressive, dominating, and from mere youthful vigor inclined to crowd out the survivors of a more ancient cycle whose territory they have only recently invaded.

Marie-Victorin (1938) subscribes to this theory of senescence to explain relic species. After studying the phytogeographic problems of eastern Canada he is

naturally led to concede the senescent condition to the allogeous flora as a whole, to consider the relics as being crowded out by a notable change in the environment, climatic or otherwise, bringing about a strong pressure from the more commonplace elements of the tundra and Spruce forest complexes.

Wynne-Edwards (1939) has found an explanation for the restricted ranges of relic species in soil preferences:

With few exceptions the rare alpine plants were shown to be basophilic, intimately correlated in their occurrence with the distribution of basic rocks. . . .

Griggs (1940), however, decided that habitat factors do not control the occurrence of rare plants when he found numerous exceptions to known habitat preferences. He cites, for instance, the fact that *Pinus Banksiana* consistently avoids limestone except in the Bruce peninsula where it grows on limestone. Griggs decided, after studying numerous rare plants, that

the difference between a rare species and a common one lies in the fact that the one fails or almost fails to establish its progeny in the competition for its habitat where the other succeeds in so doing.

The most satisfactory explanations for the occurrence of rare plants and relic species have been found by considering the limiting factors as inherent in the plants themselves rather than in the external conditions. Cain (1940),

in his criticism of the concept of species senescence has postulated satisfactory explanations based on ecological and genetic factors. He states, in part:

... each organism has a certain ecological amplitude. By this expression it is meant that an organism's range of tolerance for different intensities of a certain environmental factor is limited. . . . The plants which compose a species have approximately similar ecological amplitudes . . . it appears that genetic factors control the physiological attributes of a plant just as truly as they control the morphological attributes of the same plant . . . the capacity of a plant to vary physiologically is strictly within the inherited limits just as truly as the plant is limited morphologically by its inheritance. A plant inherits a certain ecological amplitude.

... species populations in nature are heterozygous and consist of tremendous numbers of biotypes. Within all large, wide-ranging, species populations, there are geographical partial-populations which differ genetically from other partial-populations. Evolution takes place through the isolation by one means or another of a portion of the large species population. No isolation, no speciation.

He believes that relic species:

are represented . . . by descendants from mere fragments, peripheral fragments, of the original population. . . . The common lack of colonizing ability . . . would seem to be due to their relatively greater homozygosity and consequent narrower ecological amplitude. . . .

Hultén (1937) found a cause for different genetic constitution of plants in their history during the Pleistocene. His theory was the first to emphasize inherited qualities without carrying with it the idea of age or senescence. In his study of northern vegetation Hultén, after mapping the ranges of hundreds of boreal species, finds that they fall into groups of patterns which are more or less clearly defined geographically and "equiformal." Each equiformal area shows a region of concentration of species which is called its "centre" and from this point of origin each species is assumed to have acquired its present range. The species he calls "radiants" from different "centra."

Hultén correlates the centra, as he finds them, with the distribution of ice during the Pleistocene. He finds no centra in the districts which were covered with ice during the maximum Pleistocene glaciation. Since all the plants radiate from areas that were not completely buried under the ice sheet, he suggests that it was on these "refugia" that boreal plants survived during the Pleistocene.

To explain the differences between plants having (1) relic, static and (2) general, widespread distributions, Hultén postulates some intrinsic differences between the two groups of species calling them: "plastic" and "rigid" species. The plastic species are able to migrate freely and invade new territory, whereas the rigid ones have lost their ability to pioneer and adapt themselves to new environments. Hultén does not connect the idea of senescence and age with his rigid species as Fernald does with his conservative species.

Hultén explains how the Pleistocene glaciation may have been responsible for such intrinsic, genetic differences between species:

Within a given species there is always a certain potential variation. Under the influence of a catastrophe such as the glacial period, when large parts of the area of a species in question are covered with ice and the rest is severely exposed to unfavorable conditions, a reduction of this variation is inevitable, as all biotypes, being more sensi-

tive to hardships are exterminated. . . . A very strong reduction of the biotypes is bound to ensue, and, parallel to it, a strong reduction of the potential variability and thereby also presumably the spreading capacity.

Hultén elaborates on the method by which the Pleistocene glaciation might have effected such a reduction of biotypes as follows:

That the splitting up of the earlier areas by the ice . . . must have had a very important influence on the number and character of the biotypes remaining in the different elementary areas can hardly be denied. It is evident that the selection of biotypes within the northern elementary areas must be different from that within the southern. When the ice recedes and the plants start to migrate from the isolated spots where they were left, the populations in the different elementary areas must differ in their composition. At any rate, those to the north must differ considerably from the original population which had occupied the same stations during the preceding interglacial. In other words: different races of the species must have been formed under the influence of the ice. As long as those races are separated from one another geographically they may possibly be distinguishable, but when the migration has proceeded so far that the radiants from two elementary areas meet, hybridization and thereby an integradation of the differences must be expected to occur. . . . In some of the areas isolated by the ice the conditions became so severe that certain species could not survive and therefore now show a gap in their distribution there. In other cases the plants in such an isolated area were so depauperated of biotypes that they lost their spreading capacity and are still found only in the stations where they were left by the maximum glaciation. They were thus transformed into rigid species.

Hultén's theory will explain the type of relic distribution of *Bryoxiphium* and *Brothera* as well as the widespread distribution of *Drepanocladus* and *Calliargon*. Only a few biotypes of *Brothera* and *Bryoxiphium* survived the Pleistocene whereas many of the biotypes of *Drepanocladus* and *Calliargon* may have survived. In addition, his classification of rigid and plastic species can be applied to the arctic-alpine and boreal-montane species of *Drepanocladus*. According to Hultén's theory, we can conclude that the arctic-alpine species, *D. badius*, *D. brevifolius*, *D. lycopodioides*, and *D. fluitans* var. *Berggreni*, are rigid because relatively few of their biotypes survived Pleistocene. The genetic deficiency accounts for the stability of the species and for their failure to spread from the relic localities where they persist today. We have no indication of the range of the arctic-alpine species in pre-Pleistocene times. If these species extended south from the arctic into boreal regions, then we may conclude that the Pleistocene glaciation may have been responsible for a reduction in their number of biotypes and a consequent reduction in their range. On the other hand, the arctic-alpine species may have always been restricted in their range and variability and the effect of the glacial period may have been merely to intensify an already existent condition of specific rigidity. No evidence today indicates that the arctic-alpine species ever occurred farther south than their present range, as they have never been found south of the arctic either as fossil or living plants. We are, therefore, forced to conclude that these species survived during the Pleistocene in the unglaciated parts of the arctic archipelago. Since only the biotypes adapted to that habitat exist today, the arctic-alpine species are unable to spread into other regions.

Hultén's hypothesis will also explain the existence of a stable, well-defined arctic-alpine var. *Berggreni* in the variable boreal-montane species *D. fluitans*. If only a few biotypes of var. *Berggreni* survived the Pleistocene and if these

were genetically incompatible with the rest of *D. fluitans*, then its present restricted range and stable character could be explained. The facts point to such an explanation. In North America *D. fluitans* var. *Berggreni* has been collected only on Ellesmere Island and the east coast of Greenland. Both of these areas are believed to have been free from ice during the entire Pleistocene. A few biotypes could have survived there producing the rigid population known today as var. *Berggreni*. On the contrary, *D. fluitans* has been collected south of the maximum extent of Pleistocene glaciation in Pennsylvania, West Virginia, Ohio, and New Jersey as well as on the possible nunatak, Tabletop Mountain and over the entire morainal area. *D. fluitans* is the variable, adaptable population we know today because a large number and variety of biotypes survived in numerous different habitats.

A parallel condition is found among the flowering plants in *Iris setosa*. Alaskan plants of *Iris setosa* are highly polymorphic, whereas an eastern group (var. *canadensis* Foster), isolated around the Gulf of St. Lawrence, is remarkably uniform. Anderson (1936) discusses this condition as follows:

The variation within *Iris setosa* var. *canadensis* seems particularly instructive in the light of its recent history. . . . In Alaska a large central region was left unglaciated; around the Gulf of St. Lawrence, on the other hand, the plant refuges in glacial times were little more than rocky nunataks rising above the ice. The results on the two sets of irises are just what a geneticist might predict. Even from the few specimens which are available in herbaria one can see that the *Iris setosae* of Alaska are a varied assemblage. . . . The irises of eastern Canada present a very different picture. . . . Compared to the millions of irises which might well have continued to live in Alaska during the ice age, those of the St. Lawrence were a mere handful. From that handful must have descended the millions upon millions of irises which now carpet the meadows and shores of that region. . . . Compared with our other American blue flags they are a singularly invariable lot. . . .

This conservatism of *Iris setosa* var. *canadensis* is distinctive of most of the glacial endemics (or near endemics) of the region around the Gulf of St. Lawrence. . . . In the case of *Iris setosa* var. *canadensis* the invariability cannot be a direct effect of time, for the highly variable irises of Alaska are quite as aged. It is more probably . . . an innate conservatism; a conservatism founded genetically upon the fact that these irises are descendants of a small and highly selected stock. Hard times removed from the region all the luxuriant types which may once have existed there. When the ice age was over the immediate area was repopled from the few plucky survivors. Their descendants, *Iris setosa* var. *canadensis*, bear the scars of the glacial period, so to speak, in their conservatism; an innate invariability which, on the one hand, gives them a greater uniformity, and on the other, prevents their adapting themselves readily to other environments.

The range of *D. uncinatus* var. *symmetricus* which is confined to the western mountains of America can also be explained by Hultén's rigid species resulting from selection during the Pleistocene. Evidently only the biotypes suited to the habitats of the western mountains survived the glaciation thus producing a variety confined to that geographical region today.

The boreal-montane species, *D. revolvens*, *D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. vernicosus*, and *D. uncinatus* are variable or plastic because a large number of biotypes survived the Pleistocene in a large number of areas and in a great variety of habitats. Evidence points to the conclusion that the boreal-montane species survived during the Pleistocene in all of the possible locations: (1) south of the maximum extent of the glaciation in such localities

as Lancaster County, Pennsylvania, Perry and Liberty Counties, Ohio, the Ozarks of Missouri, and Pocahontas and Preston Counties, West Virginia; (2) in the unglaciated parts of the arctic archipelago; (3) on the coastal plain in such habitats as the pine barrens of New Jersey; and (4) on unglaciated nunataks such as Tabletop Mountain and Mt. Albert in the Gaspé. The resultant genetic constitution of the boreal-montane species accounts for their variability and ability to spread into all favorable habitats. Fossil evidence shows that these boreal-montane species were as widespread during the interglacial periods (and perhaps before the Pleistocene) as they are today. It is evident, then, that there were a large number of biotypes which could have survived in unglaciated areas during the Pleistocene. In studying fossil *Drepanocladus* that have been deposited in Iowa, Minnesota, and California, it is apparent that some of the species, *D. aduncus*, *D. fluitans*, *D. revolvens*, and *D. exannulatus*, have remained unchanged since the first interglacial period. These fossil plants are so similar to plants of modern age that they have been assigned to the same varieties. Other species, *D. minnesotensis* and *D. apiculatus*, now extinct, were unable to survive, and succumbed to the vicissitudes of the Pleistocene.

In conclusion, according to the best hypotheses, the present wide distribution of *Drepanocladus* in boreal America is dependent upon the variability and adaptability of the species, and these, in turn, are dependent upon the number and variety of biotypes that survived the Pleistocene epoch.

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REFERENCES

- ANDERSON, E. 1936—The species problems in *Iris*. *Ann. Mo. Bot. Gard.* **23**:457-509.
- BLACKWELDER, E. 1931—Pleistocene glaciation in the Sierra Nevada and Basin Ranges. *Bull. Geol. Soc. Am.* **42**:865-922.
- BRAUN, E. LUCY 1928—Glacial and post-glacial plant migrations indicated by relic colonies of Southern Ohio. *Ecology* **9**:284-302.
- BRYAN, K. 1941—Correlation of the deposits of Sandia Cave, New Mexico with the glacial chronology. *Smith. Misc. Coll.* **99**(23):45-64.
- CAIN, STANLEY A. 1940—Some observations on the concept of species senescence. *Ecology* **21**:213-215.
- CHAMBERLAIN, T. C. AND R. D. SALISBURY. 1907—*Geology*, **3**, 578 pp. Henry Holt and Co., New York.
- COOPER, W. S. AND HELEN FOOT 1932—Reconstruction of a late Pleistocene biotic community in Minneapolis, Minnesota. *Ecology* **13**:63-72.
- CORE, E. L. 1932—Some aspects of the phytogeography of West Virginia. *Torreyia* **32**:65-71.

- FERNALD, M. L. 1911—A botanical expedition to Newfoundland and southern Labrador. *Rhodora* **13**:109-162.
- 1915—In Barrell, J., Factors in movements of the Strand Line and their results in the Pleistocene and post-Pleistocene, including a letter on botanical evidence by M. L. Fernald. *Am. Jour. Sci. Ser. 4*, **40**:1-42.
- 1925—Persistence of plants in unglaciated areas of boreal America. *Mem. Amer. Acad. of Arts and Sci.* **15**:241-342.
- FLINT, R. F., M. DEMOREST, AND A. L. WASHBURN 1941—Glaciation of the Shick-shock Mountains, Gaspé Peninsula. *Bull. Geol. Soc. Am.* **52**(12):1901.
- GLEASON, H. A. 1922—The vegetational history of the middle west. *Ann. Ass. of Am. Geog.* **12**:39-85.
- GRIGGS, ROBERT F. 1940—The ecology of rare plants. *Bull. Torrey Club* **67**:575-594.
- GROUT, A. J. 1930—A fossil form of *Drepanocladus fluitans* Jeanbernati (Ren.) Grout. *Bryologist* **33**:33.
- HOLZINGER, J. M. 1903—On some fossil mosses. *Bryologist* **6**:93-94.
- HULTÉN, ERIC 1937—Outline of the History of Arctic and Boreal Biota during the Quaternary Period. Their evolution during and after the glacial period as indicated by equiformal progressive areas of present plant species. 168 pp. Stockholm.
- JOHNSON, D. 1925—The New England-Acadian Shoreline. 407 pp. John Wiley and Sons. New York.
- KOCH, L. 1928—Contributions and glaciology of North Greenland. *Meddel. om Grønland* **65**(15):191-464.
- MACBRIDE, T. H. 1897—A pre-Kansan peat bed. *Proc. Iowa Acad. Sci.* **4**(1896):63-66.
- MARIE-VICTORIN, FRÈRE. 1938—Phyteogeographical problems of eastern Canada. *Am. Mid. Nat.* **19**:489-558.
- OSTENFELD, C. H. 1926—The flora of Greenland and its origin. *Det. Kgl. Danske Videns. Selskab. Biol. Meddel.* **6**(3):1-71.
- POLUNIN, N. 1940—Botany of the Canadian Eastern Arctic, Part 1. Pteridophyta and Spermatophyta. *Nat. Mus. Canada Bull.* **92**. *Biol. Ser.* 24. Canada Dept. Mines and Resources Mines and Geology Branch. 397 pp.
- POTTER, D. 1932—Botanical evidence of a post-Pleistocene marine connection between the Hudson Bay and the St. Lawrence Basin. *Rhodora* **34**:69-89; 101-112.
- PRATT, W. H. 1876—Report on a geological examination of the section of the bluffs recently exposed by the C. R. I. & P. R. R. *Proc. Davenport Acad. Nat. Sci.* **1**:96-99.
- RAUP, H. M. 1941—Botanical problems in boreal America. *Bot. Review* **7**:147-248.
- RAY, L. L. 1940—Glacial chronology of the southern Rocky Mountains. *Bull. Geol. Soc. Am.* **31**:1851-1918.
- SAVAGE, T. E. 1904—A buried peat bed in Dodge Township, Union County, Iowa. *Proc. Iowa Acad. Sci.* **11**(1903):103-109.
- 1905—Geology of Fayette County. *Iowa Geol. Surv.* **15**:433-560.
- SEIDENFADEN, F. 1931—Moving soil and vegetation in east Greenland. *Meddel. om Grønland* **87**(2):1-21.
- SHARP, AARON J. 1939—Taxonomic and Ecological Studies of Eastern Tennessee Bryophytes. *Am. Mid. Nat.* **21**:267-354.

- SIMMONS, H. G. 1913—A survey of the phytogeography of the Arctic American Archipelago with some notes about its exploration. Lunds. Universitets Arsskrift. N. F. afd. 2. **9**(19):1-183.
- STEERE, W. C. 1937—*Bryoxiphium norvegicum*, the sword moss, as a preglacial and interglacial relic. Ecology **18**:346-358.
- 1942—Pleistocene mosses from the Aftonian interglacial deposits of Iowa. Papers of the Mich. Acad. of Sci., Arts and Letters. **27**(1941):175-203.
- STEYERMARK, J. A. 1941—Studies of the vegetation of Missouri—II. Phanerogamic flora of the fresh-water springs of the Ozarks of Missouri. Bot. Ser. Field Mus. Nat. Hist. **9**(6):481-818.
- THOMPSON, ISABEL 1939—Geographical affinities of the flora of Ohio. Am. Mid. Nat. **21**:730-751.
- WELCH, WINONA H. 1936—Boreal plant relics in Indiana. Proc. Indiana Acad. Sci. **45**:78-88.
- WILLIAMS, R. S. 1930—Pleistocene mosses from Minneapolis, Minnesota. Bryologist **33**:33-36.
- WILSON, L. R. 1932—The Two Creeks Forest Bed, Manitowoc County, Wisconsin. Trans. Wisconsin Acad. Sci., Arts and Letters **27**:31-46.
- WOLFE, J. N. 1942—Species isolation and a proglacial lake in southern Ohio. Ohio Jour. Sci. **42**(1):2-12.
- WYNNE-EDWARDS, V. C. 1939—Some factors in the isolation of rare alpine plants. Trans. Roy. Soc. Canada III **33**(5):35-42.

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STUDIES IN DREPANOCLADUS III.¹

DOUBTFUL AND EXCLUDED NAMES

FRANCES E. WYNNE

Excluded varieties and forms of *D. aduncus*

²*Drepanocladus aduncus typicus* f. *aquaticus* Mönkem. in Pascher
Süßwasser-Fl. 14: 135, f. 47 d. 1914.

H. aduncum var. *aquaticum* Paris, Index 3: 607. 1896.

¹ Studies in *Drepanocladus* I. History, Morphology, Phylogeny, and Variation. Bull. Torrey Club 71 (3): [in press]. 1944. Studies in *Drepanocladus* II. Taxonomy. Brittonia 5 (2): [in press]. 1944.

² Many names have been proposed for the aquatic phase of *Drepanocladus aduncus*, *D. fluitans*, and *D. exannulatus*. Names (proposed first under *Hypnum*) such as *aquaticum*, *gracilis*, *Jeanbernati*, *laxifolium*, *paternum*, *pseudofluitans*, and *submersum* have been applied to plants of *Drepanocladus* growing submerged in water. As I have pointed out in the section on Variation in "Studies in *Drepanocladus* I" these plants are merely environmental phases produced in response to their aquatic environment. The minor quantitative characters such as size, laxness, falcateness, and distance apart of the leaves upon which the above mentioned varieties and forms were based change with changing environment. Where these names occur in the following list, reference to this footnote will indicate in each instance that the name was applied to plants of the aquatic phase. I consider these environmental fluctuations of no taxonomic significance. It is impossible to determine under which of the several varieties recognized today these names should be placed. Therefore, I am excluding them rather than placing them doubtfully in synonymy.

- ²*Hypnum aduncum* var. *Blandowii* f. *laxifolium* Sanio, Bot. Centralbl. 2(II Gratis-Beilage): 9. 1880.

Hypnum aduncum var. *flexile* Ren. in Husnot Musc. Gall. 373. 1894.

"Formes en partie émergeantes, plus grêles. Tige flexueuse. F. ordinairement plus étroites, flexueuses ou légèrement homotropes, prolongées en subule tordue" is the extent of the original description. The name was based on European material and on American material from Vancouver (Röll 144) and Calumet River, Indiana (Röll 1912, 1913). In the absence of type material the description does not give sufficient information to determine the affinities of the plant.

- ³*Drepanocladus aduncus* var. *gracilescens* Roth, Eur. Laubm. 2: 559. 1905.

Hypnum aduncum var. *gracilescens* Bry. Eur. Mon. *Hypnum* 37, pl. 605, § 1-11. 1854.

H. Kneiffii var. *gracilescens* Kindb. in Macoun Can. Cat. 7: 226. 1892.

H. tenue var. *gracilescens* v. Klinggr. Leb.-u. Laubm. v. W.-u. Ostpreuss. 272. 1893.

H. polycarpon var. *gracilescens* Limpr. Laubm. Deutschl. 3: 413. 1898.

- ³*Drepanocladus aduncus typicus* f. *gracilescens* subfo. *tenuis* Mönkem. in Pascher Süßwasser-Fl. 14: 134, f. 47 l. 1914.

Hypnum aduncum var. *tenue* Bry. Eur. Mon. *Hypnum* 36, pl. 605, § 1-5. 1854.

H. tenue v. Klinggr. Leb.-u. Laubm. v. W.-u. Ostpreuss. 272. 1893.

H. polycarpon var. *tenue* Limpr. Laubm. Deutschl. 3: 413. 1898.

Drepanocladus aduncus var. *tenuis* Roth, Eur. Laubm. 2: 560. 1905.

D. tenuis Warnst. Krypt. Mark Brand. 1008. 1906.

- Drepanocladus aduncus* var. *intermedius* Roth, Eur. Laubm. 2: 559. 1905.

Hypnum aduncum var. *intermedium* Schimp. Syn. (ed. 2) 727. 1876.

* Numerous names have been proposed for the short-celled phase of *D. aduncus*, *D. fluitans*, and *D. exannulatus*. The causes of this environmental fluctuation are discussed under the section Variation in "Studies in Drepanocladus I." As a result of certain changes in the environment, short leaves with short cells are produced. These environmental fluctuations have been given not one, but many, variety and form names including *attenuatum*, *brachydictyon*, *brevifolium*, *gracilescens*, *polycarpon*, and *tenue*. Reference to this footnote in the following list indicates the names which have been given to this short-celled phase.

The original description is as follows: "Caulis sat elongatus, parce et irregulariter pinnato-ramulosus. Folia quam maxime variabilia, e late ovata basi raptim et breviter, vel pededentim longe lanceolata, vix secunda, ramulina infima, ut in forma normali, ovata breviter acuminata, ecostata, media lanceolata, subfalcata breviter costata, summa elongato-lanceolata longe et tenuiter acuminata, vix curvata." From the illustrations which Schimper cites with the description ("Bry. eur. Suppl. III et IV, *Hypnum* tab. I, fig. 3 1-8") it is apparent that this plant is *D. aduncus* var. *typicus* which had produced some short-celled leaves toward the apex of the stems. In the *Bryologia Europaea* these figures are discussed under "Forma transitoria a typica ad var. *Kneiffii*." It is apparent, then, that Schimper realized that he was dealing with an unstable transition form. I have seen numerous plants identified as var. *intermedius* and they all belong either to var. *typicus* or to var. *Kneiffii*. I see no reason for maintaining the name *intermedius*.

Hypnum aduncum var. *Kneiffii* f. *aquaticum* Sanio, Bot. Centralbl. 2(II Gratis-Beilage): 7. 1880.

Drepanocladus aduncus var. *Kneiffii* f. *pungens* Grout, Moss Flora 3: 110. 1931.

Hypnum Kneiffii var. *pungens* H. Müll. Westfal. M. n. 247; Limpr. Kryptfl. v. Schles. 1: 68. 1877.

Drepanocladus Kneiffii var. *pungens* Roth, Eur. Laubm. 2: 561. 1905.

I have not seen the *Musci exsiccati* upon which the name *pungens* was based, but it is doubtful that a description was published there. Limpricht refers to the *exsiccati* and lists the localities in Silesia in which it had been collected. Roth and Grout give brief descriptions but include no statement of their source. Since the name is probably a *nomen nudum*, it seems best to abandon it. All of the American plants that have been identified as f. *pungens* are poorly developed *D. aduncus* var. *Kneiffii*.

Hypnum aduncum var. *platyphyllum* Paris, Index 3: 608. 1896.

H. Kneiffii var. *platyphyllum* Kindb. in Macoun Can. Cat. 6: 226. 1892.

The original description says merely "Leaves very broad and short-acuminate." This is not sufficient foundation for a variety, nor is it

enough information to determine under which of the recognized varieties of *D. aduncus* the type belongs; therefore the name is here excluded.

³*Drepanocladus aduncus* var. *polycarpus* Roth, Eur. Laubm. **2**: 559. 1905.

Hypnum polycarpon Bland. in Sturm Deutschl. Fl. Abt. 2, 13 Heft. 1818.

H. aduncum var. *polycarpum* Bry. Eur. Mon. *Hypnum* 36, pl. 605, γ 1-5. 1854.

H. psilocaulon Card. Rev. Bryol. **10**: 55. 1883.

Amblystegium polycarpum Vent. & Bott. Atti Soc. Crittog. Ital. **3**: 163. 1884.

Drepanocladus polycarpus Warnst. Beihefte z. Bot. Centralbl. **13**: 399. 1903.

D. subaduncus Warnst. Beihefte z. Bot. Centralbl. **13**: 401, 422. 1903.

³*Drepanocladus aduncus* var. *polycarpa* f. *capillifolia* Mönkem. in Pascher Süßwasser-Fl. **14**: 135, f. 47 h. 1914.

³*Drepanocladus aduncus* var. *polycarpus* f. *filicuspis* Mönkem. Laubm. Eur. 762, f. 174 c. 1927.

²*Drepanocladus aduncus* var. *pseudofluitans* Grout, Moss Flora **3**: 111. 1931.

Hypnum aduncum var. *pseudofluitans* Sanio, Bot. Centralbl. **2**(II Gratis Beilage): 7. 1880.

Drepanocladus pseudofluitans Warnst. Beihefte z. Bot. Centralbl. **13**: 405. 1903.

²*Drepanocladus aduncus* var. *pseudofluitans* f. *paternus* Grout, Moss Flora **3**: 111. 1931.

Hypnum aduncum var. *pseudofluitans* f. *paternum* Sanio, Bot. Centralbl. **2**(II Gratis-Beilage): 8. 1880.

Hypnum aduncum var. *Roellii* Ren. Hedwigia **35**: 70. 1896.

Renauld describes this plant as follows: "Tige dressée, peu rameuse ou divisée en branches fastigiées, long. 4-8 cent. F. espacées, étalées, flexueuses, les apicales lâchement dressées ou subétalées, longues de 2-3 mill., oblongues, puis insensiblement et longuement acuminées-subulées, acumen flexueux et tordu. Tissu plus ferme que d'habitude

dans le *H. aduncum*. Diffère des formes précédentes [*Hypnum aduncum* groupe *typicum* and *Kneiffii*] par ses f. beaucoup plus finement acuminées et flexueuses." Renault's type collection came from Yellowstone National Park, Wyoming (Röll 1577). It is impossible to place this variety without seeing the type material which is not in any of the larger American herbaria; therefore the name should be disregarded for the present.

Hypnum aduncum var. *rectifolium* Paris, Index 3: 609. 1896.

H. Kneiffii var. *rectifolium* Kindb. in Macoun Can. Cat. 6: 226. 1892.

Hypnum aduncum var. *Kindbergii* Paris, Index 3: 608. 1896.

Hypnum Kneiffii var. *laxum* Kindb. in Macoun Can. Cat. 6: 226. 1892.

There are no descriptions for any of these names, so they are *nomina nuda*.

²*Hypnum Kneiffii* var. *aquaticum* v. Klinggr. Leb.-und Laubm. v. W.-u. Ostpreuss. 272. 1893.

³*Hypnum Kneiffii* var. *attenuatum* Boulay, Musc. Fr. 2: 61. 1884.

Hypnum Kneiffii var. *brevifolium* C. Jens. Meddel. om Grønland 3(2): 325. 1887.

The original description says, "Folia breviora quam in [*H. Kneiffii*], caulis gracilis, parce ramosus." This is not sufficient evidence to maintain the variety; the type is not available at the present time.

Hypnum Kneiffii var. *filiforme* Berggr. K. Sv. Vet.-Akad. Handl. 13(7): 83. 1875.

Harpidium Kneiffii var. *filiforme* C. Jens. Meddel. om Grønland 3(2): 324. 1887.

Hypnum aduncum var. *filiforme* Paris, Index 3: 607. 1896.

The original description says: "Caulis tenuis regulariter pinnato-ramosus, folia ovata cuspidata, apice semitorta, subsecunda, costa ad basim crassa ad medium continua vel brevis bifurca, cellulæ alares fuscae, paucae vel nullae." There is nothing in the description to distinguish this variety. Unless examination of the type material from Greenland reveals differentiating features, the name should be abandoned.

³*Drepanocladus Kneiffii* var. *polycarpus* f. *acanthoclada* Mönkem. Laubm. Eur. 758. 1927.

Excluded varieties and forms of *D. fluitans*

³*Hypnum fluitans* (groupe *exannulatum*) var. *brachydictyon* Ren. in Husnot Musc. Gall. 385, pl. 110, f. 10, 11. 1894.

H. fluitans var. *alpinum* Ren. Rev. Bry. 8: 78. 1881. (not Schimp. Syn. 610. 1860.)

H. purpurascens var. *brachydictyon* Limpr. Laubm. Deutschl. 3: 420. 1898.

Drepanocladus fluitans var. *falcatus* Roth, Eur. Laubm. 2: 567. 1905.

Hypnum fluitans var. *falcatum* Bry. Eur. Mon. *Hypnum* 34, pl. 602, β 1, β 2. 1854.

In the Bryologia Europaea this variety is described as "lutescens vel purpurascens; foliis confertis falcato-secundis, brevioribus, angustius areolatis, costa crassiore." North American plants identified as var. *falcatus* are *D. exannulatus* var. *typicus* or *D. fluitans* var. *typicus*.

³*Hypnum fluitans* var. *hemineuron* Ren. & Card. in Husnot Musc. Gall. 388, pl. 113, f. 6-10. 1894.

Hypnum fluitans f. *terrestris* Sanio & f. *condensata* Sanio in Husnot Musc. Gall. 381. 1894.

These two varieties are treated together with the following statement: "Touffes denses, tige plus courte. C'est la forme de marécages à demi desséchés où les touffes s'étalent parfois sur la terre en formant des gazons déprimés." No distinguishing features are given. The type is from Miquelon Island (collected by Delamare) and is the only specimen known.

Drepanocladus fluitans f. *setiformis* Mönkem. in Pascher Süßwasser-Fl. 14: 139. 1914.

Hypnum fluitans var. *setiformis* Ren. in Husnot Musc. Gall. 382, pl. 109, f. 5. 1894.

The only feature distinguishing this form from var. *typicus* is that the leaves terminate in a long subulate apex. The American specimens so-named are all forms of *D. exannulatus*. Without the type, it is impossible to determine whether the name is a synonym of *D. fluitans* or *D. exannulatus*.

²*Drepanocladus fluitans* var. *submersus* Roth, Eur. Laubm. 2: 566. 1905.

Hypnum fluitans var. *submersum* Schimp. Syn. 609. 1860.

H. fluitans var. *gracile* Boulay, Musc. Fr. 63. 1884.

H. fluitans var. *Jeanbernati* Ren. Mém. Soc. d'Emul. du Doubs Ser. V. 5(1880): 50. 1881; Husnot, Musc. Gall. 380, pl. 109, f. 1, 2. 1894.

Drepanocladus fluitans f. *Jeanbernati* Warnst. Krypt. Mark Brand. 2: 1042. 1906.

Excluded forms and varieties of *D. exannulatus*

³*Drepanocladus exannulatus* var. *brachydietya* Mönkem. in Pascher Süßwasser-Fl. 14: 145, f. 49 k. 1914.

³*Drepanocladus exannulatus* var. *brachydietyon* f. *tundrac* Mönkem. in Pascher Süßwasser-Fl. 14: 145, f. 49 l. 1914.

Amblystegium tundrac Arnell, K. Sv. Vet.-Akad. Handl. 23(10): 128. 1890.

Hypnum exannulatum var. *Cochleae* Aust. Bot. Gaz. 2: 143. 1877.

Austin's description is as follows: "Caule stricto rigido parce diviso interrupte valde ramose, foliis erectis purpureo variegatis apice pro more integerrimis in siccis parte superiore spiraliter tortis, basi sensim paulo angustata distincte serrata, cellulis infimis pleurumque serie singula transversa inflatis.—*Dichelyma Swartzii*, S. & L. Exsic. Ed. 2., n. 344, planta Californica."

Variety *Cochleae* has not been mentioned in American literature since the original description; neither Grout nor Lesquereux consider it. Paris has treated the name as a synonym of *D. fluitans* var. *submersus*. Plants of No. 344 I have examined are *D. exannulatus* var. *typicus*.

Hypnum exannulatum var. *immersum* Aust. Bot. Gaz. 2: 143. 1877.

The original description says, "Caule tenue debili, foliis circinnato-falcatis tenuis perangustis, basi ut in præcedente [*H. exannulatum* var. *Cochleae*], apice distinctius remote serrato.—*Dichelyma Swartzii*, S. & L., l. c., planta Novæ Cæsarensis." Since Austin cites No. 344 for both var. *immersum* and var. *Cochleae* it is impossible to understand his concept of the two varieties. Both names are probably synonyms of *D. exannulatus* var. *typicus*.

Hypnum exannulatum var. *immersum* Paris, Index (ed. 2) 3: 34. 1904.

Harpidium exannulatum var. *immersum* C. Jens. Meddel. om Grønland 3(2): 324. 1887.

Jensen's var. *immersum* was proposed as new with the following

description: "Folia leviter v. non falcata; planta in aqua submersa." This is not sufficient information with which to decide the affinities of the plant. I have not seen the type material from Greenland, but a specimen so-named by C. Jensen from northern Europe and deposited in the New York Botanical Garden is *D. exannulatus* var. *Rotae*.

Hypnum exannulatum var. *longifolium* Paris, Index (ed. 2) 3: 35. 1904.

Harpidium exannulatum var. *longifolium* C. Jens. Meddel. om Grønland 3(2): 324. 1887.

The original description says only: "Folia elongata, vix falcata." This is hardly sufficient evidence to maintain a variety; although I have not seen the type material from Greenland, I believe this variety should be discarded.

Drepanocladus exannulatus var. *purpurascens* Dixon, Handb. Brit. Mosses 519. 1924.

Hypnum fluitans var. *purpurascens* Schimp. Syn. 609. 1860.

H. exannulatum var. *purpurascens* Milde, Bry. Siles. 349. 1869.

Harpidium exannulatum var. *purpurascens* C. Jens. Meddel. om Grønland 3(2): 324. 1887.

Hypnum fluitans (groupe *exannulatum*) var. *purpurascens* Ren. in Husnot Musc. Gall. 386, pl. 110, f. 13. 1894.

H. purpurascens Limpr. Laubm. Deutschl. 3: 418. 1898.

Drepanocladus purpurascens Roth, Eur. Laubm. 2: 563. 1905.

The only distinctive feature of this variety is its deep purple color. European or American specimens called *D. exannulatus* var. *purpurascens* are var. *typicus* or var. *Rotae*. In *Drepanocladus* color is obviously a result of exposure to sunlight and is not a satisfactory character upon which to base varieties. I am proposing, therefore, that var. *purpurascens*, based only on color, be excluded, and only varieties determined by more dependable characters of cells and leaves be retained.

Amblystegium exannulatum var. *tenellum* C. Jens. Meddel. om Grønland 15(7): 432. 1897.

The original description, "Gracillima, humilis, simplex vel parce ramosa foliis brevioribus," is so vague that, although I have not seen the type from Greenland, I am excluding this variety.

Drepanocladus exannulatus f. *obtusa* Mönkem. in Pascher Süßwasser-Fl. 14: 144. 1914.

Mönkemeyer says. "Blätter kürzer mit rundlich abgestumpfter

Spitze." I have seen no American plants with obtuse apices. This name has been used by American authors for the short-celled phase of *D. exannulatus*. The name may be disregarded insofar as American material is concerned.

Drepanocladus exannulatus f. *orthophyllus* Mönkem. in Pascher Süsswasser-Fl. 14: 144. 1914.

Hypnum exannulatum var. *orthophyllum* Milde, Bry. Siles. 349. 1869.

The original description is as follows: "Tracht ganz der vorigen Varietät [*purpurascens*] und mit dieser in Gesellschaft, aber die Blätter ganz aufrecht und kürzer zugespitzt." It is impossible to determine, from the meager description from what varietal base this form might have been developed. American plants identified as f. *orthophyllus* have been the short-celled phase of both var. *typicus* and var. *Rotae*.

Drepanocladus exannulatus f. *tenuis* Mönkem. in Pascher Süsswasser Fl. 14: 144. 1914.

The name *tenuis* has been applied to very slender reduced forms which are the merest habitat variations.

Drepanocladus Rotae var. *falcifolius* Warnst. Krypt. Mark Brand. 1049. 1906.

Hypnum exannulatum var. *falcifolium* Ren. in Husnot Musc. Gall. 387, pl. 111, f. 4, 5. 1894.

Any plant of *D. exannulatus* var. *typicus* could fit Renault's description of var. *falcifolius*. Only one distinctive characteristic is mentioned in the original description: "F. . . . rétrécies en une longue subule souvent roulée en spirale . . ." Renault further states ". . . . habituellement purpurescent et trapue, parfois avec des feuilles serrées de façon à passer par des transitions à la var. *purpurascens*." Without question the original plant was *D. exannulatus* var. *typicus*. I do not know on what authority Warnstorf included it under *D. Rotae*. Variety *falcifolius* has been reported from North America from Montana and Wyoming, but the plants are *D. exannulatus* var. *typicus*.

Hypnum exannulatum var. *Swartzii* Aust. Bot. Gaz. 2: 143. 1877.

Dichelyma Swartzii Lindb. in Hartm. Skand. Fl. (ed. 8) 353. 1861. Austin describes var. *Swartzii* in the same paragraph with var.

immersum and var. *Cochleae* as follows: "Foliis hamato-incurvis rigidis (subserratis) basi solidioribus, cæteroquin ut in præcedente.—*Dichelyma Swartzii*, Lindb!" His material was probably *D. exannulatus* var. *typicus*. I have not seen Lindberg's type material.

Excluded forms and varieties of *D. uncinatus*.

⁴*Drepanocladus uncinatus* var. *abbreviatus* Warnst. Beihefte z. Bot. Centralbl. 13: 420. 1903.

Hypnum uncinatum var. *abbreviatum* Bry. Eur. Mon. *Hypnum* 31, pl. 600, § 1, § 2. 1854.

Hypnum uncinatum var. *subsulcatum* Warnst. Hedwigia 26: 55. 1887.

The description of var. *abbreviatum* is "demissum, intricato-caespitosum; caule brevior, foliis angustioribus magis falcatis, capsula in pedicello dimidio brevior."

Drepanocladus uncinatus var. *alpinus* Warnst. Krypt. Mark Brand. 2: 1033. 1906.

Hypnum uncinatum var. *subjulaceum* f. *alpina* Ren. in Husnot Musc. Gall. 379, pl. 108, f. 12. 1894.

This name has been applied to American material, but plants so called are small *D. uncinatus* var. *typicus*.

⁴*Drepanocladus uncinatus* var. *gracilescens* Roth, Eur. Laubm. 2: 551. 1905.

Hypnum uncinatum var. *gracilescens* Bry. Eur. Mon. *Hypnum* 31, pl. 600, § 1. 1854.

This variety was originally described as "densius caespitosum; caule erecto gracili, confertim pinnato-ramulosum, foliis dimidio fere minoribus, minus falcatis" and later expanded by Renauld and Warnstorf to include plants with leaves falcate but not circinate, slightly plicate, and subentire.

⁴ These varieties are based on small plants and it is impossible to separate them by means of the original descriptions. It is possible to find plants which fit some of the characters, but at the same time, it is also possible to find in the same collection typical plants and all intergradations. Leaves of various lengths (2.2, 2.4, 2.5, 3.0, 3.2 mm.) were found in the same clone. The leaves also vary in the regularity and strength of the plications, the amount of serrulation, and the strength of the costa. In all collections, however, typical *D. uncinatus* plants can be found. From these observations it is apparent that the forms called *abbreviatum*, *gracilescens*, *gracillimum*, *plumosum*, and *plumosum* are variations of no significance except as minor habitat forms. All collections in which these small plants were found were from the north, so they may be explained as the reduced, delicate forms so commonly produced in that region.

⁴*Hypnum uncinatum* var. *gracillimum* Berggr. K. Sv. Vet.-Akad. Handl. **13**(7): 86. 1874.

Harpidium uncinatum var. *gracillimum* Lange et C. Jens. Meddel. om Grønland **3**(2): 323. 1887.

“Dense caespitosum, caulis tenuis filiformis, parce ramosus, folia ovata cuspidata, cellulis latioribus, nerve brevioris,” is the original description.

Amblystegium uncinatum var. *Hartii* C. Jens. Meddel. om Grønland **15**(7): 431. 1897.

The original description says merely: “Autoica, subtus fusca, versus apicem auronitens. Folia plicis longitudinalibus, omnia eleganter et fortiter secundo-uncinata; cellulae alariae parietibus crassis, plus minusve luteofuscis, non translucidis.” I have not seen the type material from Scoresby Sound and cannot distinguish this variety from *D. uncinatus* var. *typicus* by means of the original description.

⁴*Drepanocladus uncinatus* var. *plumosus* Warnst. Beihefte z. Bot. Centralbl. **13**: 421. 1903.

Hypnum uncinatum var. *plumosum* Schimp. Syn. 612. 1860.

The original description for this variety is: “demissum, longe prorepens, molle, pinnato ramulosum, foliis hamatis acumine capillaceo longiore flexuso, capsula angustiore, incurvo-cylindracea.”

⁴*Drepanocladus uncinatus* var. *plumulosus* Warnst.—Beihefte z. Bot. Centralbl. **13**: 421. 1903.

Hypnum uncinatum var. *plumulosum* Bry. Eur. Mon. *Hypnum* 31, pl. 600 γ 1, γ 2. 1854.

Amblystegium uncinatum var. *plumulosum* Sanio, K. Sv. Vet.-Akad. Handl. **23**(10): 118. 1890.

Variety *plumulosum* was originally described as “tenellum, molle, omnino repens; ramulis magis confertis; capsula in pedicello brevi minore,” and the name has been used for plants with leaves slightly or not at all striate and hardly serrulate at the apex.

Excluded species of *Drepanocladus*

Hypnum conflatum C. M. & Kindb. in Macoun Can. Cat. **6**: 230. 1892.

The original description is as follows: “Allied to *Hypnum Kneiffii*. Stem slender, subfiliform, distantly pinnate, not radiculose. Leaves small, concave, distant, denticulate all around; stem-leaves decurrent, from a broad-ovate base suddenly narrowed into a very short, sub-

ulate-filiform, straight point; alar cells very large, hyaline or faintly yellowish, the other nearly uniform, oblong-lanceolate, conflated; costa pale-yellow, vanishing in the acumen; branch-leaves narrower, oblong-lanceolate, more or less short-acuminate, curved or straight. Capsule very small, arcuate and contracted below the mouth. Dioecious."

Several collections are cited with the original description as types, including John Macoun, *Canadian Musci* 334 & 336 "in part." It is impossible to know which parts were described. The specimens of these numbers which I examined were *Drepanocladus aduncus* var. *typicus*.

Drepanocladus Sendtneri Warnst. Beihefte z. Bot. Centralbl. 13: 400. 1903.

Hypnum Sendtneri Schimp. Musci Eur. Novi *Hypnum* 2, 3. pl. 2. 1866.

Amblystegium intermedium var. *Sendtneri* Vent. & Bott. Atti. Soc. Crittog. Ital. 3: 164. 1884.

A. Sendtneri de Not. Epil. 139. 1869.

Drepanocladus Sendtneri f. *aristinnervis* Mönkem. Laubm. Eur. 786. f. 176 d. 1927.

Drepanocladus Sendtneri f. *gracilescens* Grout, Moss Flora 3: 112. 1931.

Hypnum aduncum var. *legitimum* var. *gracilescens* Sanio, Bot. Centralbl. 2(II Gratis-Beilage): 14. 1880.

Drepanocladus Sendtneri var. *Wilsoni* Grout, Moss Flora 3: 112. 1931.

Hypnum Wilsoni Schimp. in Ltz. Bry. Notizb. 76. 1865.

H. intermedium var. *Wilsoni* Lindb. Spitzb. Mossor. 540. 1866.

Amblystegium Sendtneri var. *giganteum* de Not. Epil. 139. 1869.

A. Wilsoni Lindb. M. Scand. 33. 1879.

Harpidium Wilsoni C. Jens. Meddel. om Grønland 3(2): 325. 1887.

Hypnum lycopodioides subsp. *H. Wilsoni* Ren. in Husnot Musc. Gall. 375. 1894.

Drepanocladus Wilsoni Roth, Eur. Laubm. 2: 554. 1905.

D. Sendtneri f. *Wilsoni* Mönkem. in Pascher Süßwasser-Fl. 14: 136. 1914.

Hypnum Wilsoni var. *americanum* Ren. in Husnot. Musc. Gall. 376, pl. 111, f. 1. 1894.

Hypnum Wilsoni var. *occidentale* Ren. & Card. in Husnot Musc. Gall. 394, pl. 111, f. 9-11. 1894.

I have seen no American plants that correspond to the original description of *D. Sendtneri* or its several varieties. Specimens so-named are *D. exannulatus*, *D. fluitans*, *D. aduncus*, *D. uncinatus*, or *D. revolvens*. The only distinctions mentioned in the original description between *D. aduncus* and *D. Sendtneri* are the more robust habit and the incrassate basal and alar cells of the latter. In other characters of sporophyte, leaf, and stem the two species are similar. A study of European material available also shows that *D. Sendtneri* is synonymous with *D. aduncus*.

In some submerged plants of *D. aduncus*, the basal and alar cells may be incrassate and colored, but the upper leaves have the areolation typical of *D. aduncus*. I think it quite possible that the original description of *D. Sendtneri* is of old submerged leaves of robust plants of *D. aduncus*. In any event, a large number of the specimens called *D. Sendtneri* are robust, aquatic plants of *D. aduncus* var. *typicus*.

The specimens filed under *D. Sendtneri* are the most heterogeneous assortment of species of *Drepanocladus* imaginable. Therefore, it is suggested that the species with all its varieties and forms be excluded.

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STUDIES IN DREPANOCLADUS. IV. TAXONOMY¹

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The genus *Drepanocladus* belongs to the subfamily Amblystegieae of the Hypnaceae. Nine species of *Drepanocladus* are recognized in this treatment: *D. aduncus*, *D. fluitans*, *D. exannulatus*, *D. uncinatus*, *D. revolvens*, *D. lycopodioides*, *D. vernicosus*, *D. badius*, and *D. brevifolius*. Three varieties of *D. aduncus* are recognized: var. *typicus*, var. *Kneiffii*, and var. *capillifolius*; two varieties of *D. fluitans* are recognized: var. *typicus* and var. *Berggreni*; two varieties are recognized for *D. exannulatus*: var. *Rotae* and var. *typicus*; and three varieties are recognized for *D. uncinatus*: var. *typicus*, var. *subjulaceus*, and var. *symmetricus*. *D. Berggreni* has been reduced to a variety of *D. fluitans*, *D. intermedius* to a synonym of *D. revolvens*, and *D. Sendtneri* has been excluded.

Drepanocladus aduncus, *D. fluitans*, and *D. exannulatus* are the most variable species in the genus and hence have accumulated not only more synonyms but also more varietal and formal names than the other species. Most of the described varieties and forms of these species intergrade continuously. The distinctions, if present at all, are extremely difficult to see and still more difficult to define. It has been possible, therefore, to reduce the number of recognized varieties and forms without sacrificing any nomenclatural precision. It is natural that the first studies of a variable group should result in the proposal of a large number of names. When the extremes of a species are first seen, and the intergrading forms are unknown, or imperfectly understood, it has been customary to give them nomenclatural recognition. When, with more study and collecting, the connecting forms also become known, it is possible to see the relationship of the extremes to the normal. Therefore, I have been able to reduce very considerably the number of varieties and forms in several species reported from North America. Field studies of the environmental adaptations of *Drepanocladus* have led to a better understanding of the nature of variation in the genus. Many of the so-called varieties and forms of *Drepanocladus* have been shown to be merely environmental phases resulting from the fluctuations of plastic, adaptable species.²

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² Bull. Torrey Club 71: 207-225. f. 1, 2. 1944.

The varieties recognized in *Drepanocladus* have been based, in this treatment, upon hereditary variations. The methods of determining which characters were the expression of hereditary factors and which resulted from a response to environmental conditions have been discussed in a previous paper.² The "short-celled phase" and "aquatic phase" mentioned in the following pages are produced by changes in the environment.³ For *D. aduncus*, *D. fluitans*, *D. exannulatus*, and *D. uncinatus*, each of which has several varieties, I have included a variety *typicus*. However, in the other species, which are so stabilized that several varieties apparently do not exist, I consider it unnecessary to propose a variety *typicus*.

Exsiccati are cited geographically according to states and provinces from east to west and from north to south, and abbreviated as follows:

Grout, North American Musci Pleurocarpi—N. A. M. Pl.

Grout, North American Musci Pleurocarpi Supplement—N. A. M. Pl. Suppl.

Grout, North American Musci Perfecti—N. A. M. Perf.

John Macoun, Canadian Musci—Can. Musci.

W. S. Sullivant & L. Lesquereux, Musci Boreali Americani—M. Bor. Am.

J. A. Allen, Mosses of the Cascade Mountains—Cascade Mts.

Coe Finch Austin, Musci Appalachiani—M. App.

J. A. Moore and J. Steyermark, Plants of Grand Teton National Park—Grand Teton Nat. Park

Thomas Howell, Pacific Coast Plants—Pac. Coast.

Renauld & Cardot, Musci Americae Septentrionalis Exsiccati—M. Am. Sept.

Complete mimeographed lists of the specimens examined may be obtained from the author on request. The distribution maps for each species show the actual localities for all collections examined.

The following symbols adapted from *Chronica Botanica* (5: 142-150. 1939) have been used in referring to specimens in the various herbaria:

(BART)—E. B. Bartram, Bushkill, Pa.

(DUKE)—Dr. A. J. Grout's herbarium, now at Duke University, Durham, N. C.

(MICH)—University of Michigan, Ann Arbor.

(NY)—New York Botanical Garden.

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³ For a detailed discussion of these habitat phases and the excluded names see *THE BRYOLOGIST* 47: 66-78. 1944.

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DREPANOCLADUS (C. Müll.) Roth, Beiblatt z. Hedwigia **38**: 6. 1899; Warnst. Beihefte z. Bot. Centralbl. **13**: 397. 1903.

Hypnum sp., Dill. Hist. Musc. 292. 1741.

Hypnum Sect. IV *Mallacodium* Subsect. I. *Drepanocladus* C. Müll. Syn. **2**: 321. 1851. (ex. *H. riparium*).

Hypnum subg. 12. *Harpidium* Sull. Musc. and Hep. U. S. 73. 1856.

Amblystegium subg. *Macrophylla* DeNot. Epil. 130. 1869.

Amblystegium C. *Drepanocladus* Lindb. Musc. Scand. 32. 1879.

Amblystegium subg. *Harpidia* Vent. & Bott. Atti. Soc. Crittog. Ital. **3**: 163. 1884.

Harpidium Lange & C. Jensen, Meddel, om Grønland **3** (2): 321. 1887.

Dioicous or monoicous. Plants slender and soft, or robust and stiff, varying in color: golden, yellow-green, green, red, crimson, purple, brown, or black; stems erect, creeping, or floating, 1–30 cm. long, simple, irregularly fastigiately branched or regularly pinnately branched, 2–4 mm. in diameter, showing a small central strand in cross-section (except *D. vernicosus*); branches 2–25 mm. long, apical buds of stems and branches falcate-secund to circinate (almost straight in *D. aduncus* var. *Kneiffii*); pseudoparaphyllia in the axils of the leaves of *D. uncinatus*; radicles rarely on stems or leaves (frequently on *D. fluitans* and *D. badius*).

Stem leaves broadly ovate, lanceolate, or linear-lanceolate, abruptly short-acuminate or gradually long-acuminate, $1.0\text{--}6.0 \times 0.3\text{--}1.0$ mm., clasping the stem at intervals of 0.1–0.9 mm., secund or strongly and regularly circinate (straight in *D. aduncus* var. *Kneiffii*); not decurrent or with auricles strongly decurrent; regularly and strongly plicate, irregularly plicate, striate, or plane; margin serrulate, sinuate, or entire; line of insertion of leaf straight, slightly or deeply concave, or circular; transition of cells of stem to cells of leaf gradual or abrupt as seen when cortical stem cells remain attached to the base of the leaf. Costa single, green or deeply colored, extending $\frac{1}{3}\text{--}\frac{4}{5}$ the length of the leaf or long and excurrent. Branch leaves similar to stem leaves but smaller.

Cells long and narrow, linear (short and broad in habitat phases of *D. aduncus*, *D. fluitans*, and *D. exannulatus*), median leaf cells 4–6 μ .

× 40–120 μ , thin walled or incrassate and pitted in basal region (all cell walls incrassate in *D. lycopodioides* and *D. badius*; all cell walls pitted in *D. badius* and *D. brevifolius*); alar cells poorly or well delimited, quadrate or inflated, hyaline or colored, confined to the basal angles or extending across the entire base of the leaf.

Antheridial buds produced on the primary stems; perigonial bracts ovate, briefly acuminate, ecostate or with a short, weak costa; antheridia ovate-oblong; paraphyses of 4–6 cells. Perichaetium 3–6 mm. long, sheathing the base of the seta; outer perichaetial leaves ovate, ecostate or with a weak costa; inner perichaetial leaves lanceolate, abruptly to gradually acuminate, smooth to regularly plicate; costa extending $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf.

Seta 3–10 cm. long, red to brown; capsule 1.4–3.0 mm. × 0.6–1.0 mm., smooth or plicate, asymmetric (or symmetric in *D. uncinatus* var. *symmetricus*), slightly contracted under the mouth when dry and empty; exothecial cells smooth or mamilliose; operculum rostrate or apiculate, 0.4–0.8 mm. high; annulus present and persistent (lacking in *D. fluitans* and *D. exannulatus*); peristome perfect; outer peristome yellow to red, inner peristome pale to yellow, cilia 2–3. Spores yellow-green to olive, papillose or smooth, 12–20 μ in diameter.

TYPE SPECIES: *Hypnum aduncum* Hedw.

Although many of the species of *Drepanocladus* are extremely variable, the genus itself is distinctive. The outstanding diagnostic features of *Drepanocladus* are its falcate leaves with a single costa and acute apex, the long-linear areolation, and characteristic alar cells. *D. aduncus* var. *Kneiffi* and the habitat phases with straight leaves can be recognized as belonging to *Drepanocladus* by their slightly falcate-second apical buds, single costa, acute apex, and inflated alar cells. Such forms are confused with *Leptodictyum* which is, in general, of more flattened, spreading habit and without inflated alar cells. In general, *Hygrohypnum* is to be distinguished from *Drepanocladus* by its variable costa which may be long and single on some leaves or short and double on other leaves of the same plant. *Amblystegium* and *Hygroamblystegium* are distinguished from *Drepanocladus* by their stronger costae, the more abruptly acute leaves, and shorter cells. Stems of both *Hygrohypnum* and *Hygroamblystegium* are often denuded of leaves at the base; this is never true in *Drepanocladus* for no matter how old the stems nor how deeply submerged, they are always leafy to the base. *Cratoneuron* is separated from *Drepanocladus* by the abundant paraphyllia on the stems. Although the habit of *Scorpidium* resembles a large *Drepanocladus*, the costa is short and double or wanting.

With the exception of *D. uncinatus*, all the species of *Drepanocladus* are aquatic or semi-aquatic. Some of the species occur in semi-aquatic habitats, such as moist depressions in meadows, woods, old river beds, tussocks in swamps, around the base of reeds and grass in marshes and swamps. Others are most frequent in strictly aquatic habitats as pools and stagnant water in swamps, bogs, and meadows, beach pools, ditches, sluggish streams, ditches, sloughs, and swales. In contrast to all the other species of *Drepanocladus*, which are hydrophytic, *D. uncinatus* grows in mesophytic or xerophytic habitats.

KEY TO SPECIES AND VARIETIES

Leaves entire

Alar cells inflated forming conspicuous groups at the basal angles; cortical stem cells gradually intergrading with the leaf cells.

Costa excurrent.....*D. aduncus* var. *capillifolius*.

Costa ending in acumination.

Leaves secund, apex channelled.....*D. aduncus* var. *typicus*.

Leaves straight, (apical buds secund) apex flat.....*D. aduncus* var. *Kneiffii*.

Alar cells not inflated, sometimes incrassate or colored.

Walls of some cells thickened, porose, and colored; plants golden or reddish to black; stems with a central strand.

Walls of basal cells porose and colored.

Cells of cortex of stem not enlarged; all cell walls incrassate; plant deep golden, large.....*D. lycopodioides*.

Cells of cortex of stem enlarged; basal cells incrassate; plants green or reddish to black.....*D. revolvens*.

Walls of all cells porose.

Cell walls incrassate.....*D. badius*.

Cell walls not incrassate; costa thin, sometimes double and forking.....*D. brevifolius*.

Walls of all cells thin, not porose; plant clear green; stems without a central strand; leaves irregularly plicate

D. vernicosus.

Leaves serrulate at either apex or base or both.

Leaves strongly and regularly plicate; alar cells quadrate....*D. uncinatus*.

Leaves plane, alar cells inflated.

Alar cells poorly differentiated in small groups—never extending to costa.

Plants small (leaves 1.2–1.6 mm. $\times$ 0.4–0.6 mm.), costa variable, single or short and double....*D. fluitans* var. *Berggreni*.

Plants large (leaves 2.0–4.0 mm. $\times$ 0.3–1.0 mm.), costa always single.....*D. fluitans* var. *typicus*.

Alar cells forming large groups always extending to the costa.

Costa excurrent.....*D. exannulatus* var. *Rotae*.

Costa ending in the acumination.....*D. exannulatus* var. *typicus*.

DREPANOCLADUS ADUNCUS (Hedw.) Warnst. Beihefte. z. Bot. Centralbl. 13: 400. 1903.

Hypnum aduncum Hedw. Sp. Musc. 295. 1801; Bry. Eur. Mon.

Hypnum Suppl. p. 1, pl. 1. 1866.

Amblystegium aduncum DeNot. Comment. Crittogam. Ital. 2(3): 290. 1867.

Dioicous. Plants green, yellow-green, golden or brownish, never reddish or deeply colored; varying in habit, stems creeping, erect, or floating, usually slender and soft, 1–30 cm. long, simple or with branches short and fastigiate or long and plumose, 2–25 mm. long, irregularly to regularly pinnate; apical buds of stems and branches almost straight in var. *Kneiffii* or falcate-secund in var. *typicus* and var. *capillifolius*, not circinate.

Stem leaves clasping the stem at intervals of 0.2–0.5 mm. (0.1–0.9 mm.), usually decurrent at the auricles, not plicate but sometimes irregularly striate, falcate, not circinate in var. *typicus* and var. *capillifolius*, straight, not falcate, in var. *Kneiffii*, ovate-lanceolate, oblong-lanceolate or long-lanceolate, short and abruptly acuminate from a broadly lanceolate base, or gradually long-acuminate from a long-lanceolate base in var. *typicus* and var. *Kneiffii*, 2.0–3.5 mm. $\times$ 0.6–0.8 mm. (1.0–5.5 mm. $\times$ 0.3–1.0 mm.); line of insertion of leaf widely concave to circular, depending on the width of the leaf at the base and the degree of clasping; transition of cells of stem to cells of leaf gradual, as seen when a few cortical stem cells remain attached to the base of the leaf; margin entire or faintly sinuate at base; costa extending $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf in var. *Kneiffii* and var. *typicus*, or excurrent in var. *capillifolius*, green, 40 μ (20–120 μ) wide at base. Branch leaves similar to stem leaves but smaller, 1.0–2.8 mm. $\times$ 0.2–0.5 mm. (0.5–3.5 mm. $\times$ 0.2–0.9 mm.).

Cells linear, thin walled, median leaf cells 4–6 μ $\times$ 40–60 μ (4–8 μ $\times$ 20–100 μ), alar cells inflated, large, hyaline or colored, 3–4 ranks high at margin, forming distinct dorsally ventricose auricles extending $\frac{1}{4}$ – $\frac{1}{2}$ of the distance from the margin to the costa (sometimes reaching the costa in var. *capillifolius* and submerged plants of var. *typicus* and var. *Kneiffii*), 12–16 μ $\times$ 40–60 μ (8–20 μ $\times$ 32–120 μ).

Antheridial buds in the axils of the leaves on the primary stems, perigonal leaves ovate, 0.5–0.8 mm. $\times$ 0.2–0.4 mm., costa short, extending half the length of the leaf; antheridia 2–4, small, 0.3 mm. long, paraphyses short, 3–4 cells long. Perichaetium 4 mm., sheathing the base of the seta; perichaetial leaves broadly lanceolate, spreading, abruptly piliform, 2.4–2.6 mm. $\times$ 0.8–1.0 mm., costa extending half the length of the leaf; inner perichaetial leaves broadly lanceolate; abruptly piliform, costa extending half the length of the leaf, 2.8–3.2 mm. $\times$ 0.5–0.7 mm.

Seta 2–6 cm. long; capsule arcuate, oblong, 2.3–2.8 mm. $\times$ 0.4–0.6 mm., contracted under the mouth, exothecial cells 24 $\times$ 32 μ toward the mouth of capsule, isodiametric (20 μ) at base, mamilliose, operculum conic, 0.7 mm. high; annulus persistent, of three rows of cells; outer peristome deep yellow, inner peristome pale, cilia paired. Spores papillose, yellow-green, 16 μ in diameter.

TYPE LOCALITY: Europe.

HABITAT: Pools in swamps, bogs, and meadows; beach pools, lakes, sluggish streams, ditches, sloughs, swales; moist depressions in meadows, woods, old-river beds; among reeds and grass in marshes; on tussocks in swamps. All the varieties of *D. aduncus* will grow in calcareous places although apparently lime is not necessary. *D. aduncus* occurs more commonly in calcareous places than any other species of *Drepanocladus*.

GENERAL DISTRIBUTION: Circumpolar. In the northern hemisphere throughout northern Europe, Asia, and North America and southward along the mountain ranges; Greenland, Iceland. In the southern hemisphere in northern Africa, the Andes of Peru, and New Zealand. In North America throughout the arctic south to New Jersey, Pennsylvania, Ohio, Missouri, Iowa, Nebraska, New Mexico, Utah, and California (Map 1).

Drepanocladus aduncus is distinguished by its plane, entire, broadly lanceolate leaves, its large group of dorsally ventricose alar cells, and rather broad, short leaf cells. Although *D. aduncus* is an extremely protean species and exceedingly variable, it can readily be distinguished from the allied species of the genus. *D. exannulatus* is distinctive in its deep color, stout habit, and long-linear leaves with the alar cells extending to the costa. *D. vernicosus* is plicate, with a short blunt acumen and no inflated alar cells. *D. revolvens*, likewise, has no inflated alar cells and characteristically is red with strongly circinnate leaves. *Drepanocladus aduncus* can be distinguished from *D. fluitans*, its closest relative and with which it is most often confused, by its entire margin, broad leaves, wider, shorter cells, and the gradual transition from cells of the stem to cells of the leaf. When the leaves of *D. aduncus* are removed from the stems, some of the cortical stem cells usually remain attached to the base of the leaf as long or short "tails" and it is easily seen that the stem cells intergrade completely with the leaf cells. Typically the leaves of *D. aduncus* are more strongly secund than leaves of *D. fluitans*. The areolation in *D. aduncus* is shorter and more lax than in *D. fluitans*—the median leaf cells are $4-6\ \mu \times 40-60\ \mu$ in contrast to $4-6\ \mu \times 64-80\ \mu$ in *D. fluitans* var. *typicus*. The cells at the apex of the leaves of *D. aduncus* are much shorter than in *D. fluitans*. *D. fluitans* with its poorly developed auricles, never has the large inflated, dorsally ventricose alar cells of *D. aduncus*.

DREPANOCLADUS ADUNCUS var. **typicus** (Ren.) Wynne, stat. nov.

Hypnum aduncum f. *typica* Ren. in Husnot Musc. Gall. 368
pl. 105, f. 4, 5, 6, 7. 1894.

H. aduncum f. *falcata* Ren. in Husnot Musc. Gall. 369, pl. 105,
f. 8. 1894.

Drepanocladus aduncus typicus Mönkem. in Pascher Süßwasser-
Fl. 14: 134, f. 47 a, b. 1914.

Plants green or yellow-green, growing erect, creeping, or submerged; stems slender and soft, 3–10 cm. long (15–30 cm. long in submerged plants), simple, irregularly or regularly pinnately branched, branches 3–10 mm. long, apical buds of stems and branches falcate-secund.

Stem leaves clasping the stem at base, 0.2–0.6 mm. apart on the stem, decurrent at the auricles, not plicate, sometimes irregularly striate, falcate, oblong-lanceolate, gradually acuminate from a lanceolate base, 2.0–3.5 mm. $\times$ 0.6–0.8 mm. (1.0–2.8 mm. $\times$ 0.4–0.6 mm. in the small short-celled phase; 3.0–5.4 mm. $\times$ 0.6–1.0 mm. in submerged plants), apex channelled because of the secunity of the leaves, insertion of the leaf widely concave, narrowly concave or circular, margin entire; costa extending well into the acumen, not excurrent, green; 40 μ (20 μ in the short-celled phase; 40–120 μ in the aquatic phase) wide at base. Branch leaves similar to the stem leaves but smaller, 1.0–2.0 mm. $\times$ 0.4–0.5 mm.

Cells linear, thin-walled, median leaf cells 4–6 μ $\times$ 40–60 μ (4–6 μ $\times$ 28–32 μ in the short-celled phase; 4–6 μ $\times$ 40–80 μ in the aquatic phase); alar cells inflated, large, hyaline, forming distinct auricles extending $\frac{1}{4}$ – $\frac{1}{2}$ the distance from the margin to the costa, 12–16 μ $\times$ 40–60 μ .

Renauld was the first to indicate a concept of the typical *D. aduncus*. One of his "groupes" under *Hypnum aduncum*, in his treatment of Section *Harpidium* in Husnot's "Musculologia Gallica," is "Groupe typicum." Here he described and illustrated (pl. 105) "forma typica (e specimine Hedwigii)." Since he was evidently following Hedwig's conception of *H. aduncum* I have used his name "typicum" for *D. aduncus* var. *typicus*. Mönkemeyer, in Pascher's "Süßwasser-Flora" uses "*D. aduncus typicus*" but he does not indicate the varietal rank.

ILLUSTRATIONS: Husnot, Musc. Gall., short-celled phase—pl. 105, f. 10, 11; pl. 106, f. 4, 6, 8; aquatic phase—pl. 105, f. 12; Pascher, Süßwasser-Fl. 14: 133, short-celled phase—f. 47 k, l; aquatic phase—f. 47 d. 2 ed. 14: 155, short-celled phase—f. 54 a, c, d; 156, f. 55 c; aquatic phase—153, f. 53 f; Mönkemeyer, Laubm. Eur., short-celled phase—759, f. 173 a, c, d; 156, f. 55 c; aquatic phase—756, f. 171 f.

EXSICCATI—*D. aduncus* var. *typicus*: VERMONT: N. A. M. Pl. 326 (DUKE); N. A. M. Perf. 60 (BART); CONNECTICUT: N. A. M. Pl. 356 (DUKE, BART); N. A. M. Pl. 475 (MICH, BART, NY); PENNSYLVANIA:

M. Bor. Am. Ed. 2, 1865, 467, 316b (MICH); OHIO: M. Bor. Am. Ed. 1, 1856, 316 (MICH); ILLINOIS: N. A. M. Pl. 289 (MICH, NY); MINNESOTA: N. A. M. Pl. 249 (DUKE, MICH); NORTH DAKOTA: N. A. M. Pl. 394 (DUKE, BART); COLORADO: N. A. M. Pl. 365 (DUKE, BART); WASHINGTON: N. A. M. Pl. 216 (DUKE); Cascade Mts. 136 (BART); Plants of the State of Washington 843 (MICH, NY); CALIFORNIA: N. A. M. Pl. 13 (NY, DUKE); QUEBEC: N. A. M. Pl. 423 (DUKE, BART, NY); N. A. M. Pl. 423a (DUKE, BART, NY); N. A. M. Pl. 454 (DUKE, BART, MICH, NY); N. A. M. Pl. 426 (DUKE, BART); N. A. M. Pl. 433a, (DUKE, BART, NY); N. A. M. Pl. 431 (BART, DUKE, NY); N. A. M. Pl. 389a (DUKE, MICH, NY); ONTARIO: Can. Musci 336 (NY); M. Am. Sept. 395 (NY); BRITISH COLUMBIA: Can. Musci 846a (DUKE); N. A. M. Pl. Suppl. 23 (DUKE, BART, NY); N. A. M. Pl. Suppl. 20 (DUKE, BART, NY); Can. Musci 658 (NY); Can. Musci 447 (NY); Can. Musci 847 (NY).

DREPANOCLADUS ADUNCUS var. *KNEIFFII* (Bry. Eur.) Mönkem. in Pascher Süsswasser-Fl. (2 ed.) 14: 153, f. 53b. 1931; Grout, Moss Flora 3: 110. 1931.

Amblystegium Kneiffii Bry. Eur. Mon. *Amblystegium* 17, pl. 573. 1853.

Hypnum Kneiffii Schimp. Coroll. 135. 1855.

H. aduncum var. *Kneiffii* Schimp. Syn. (2 ed.) 727. 1876.

Drepanocladus Kneiffii Warnst. Beihefte z. Bot. Centralbl. 13: 399. 1903.

Plants green to brownish, stems usually slender and soft, creeping, erect, or floating, 1–30 cm. long, simple, or with short branches, 3–10 mm. long, irregularly to regularly pinnate, apical buds of stems and branches only slightly falcate-secund.

Stem leaves clasping the stem, 2–5 mm. distant, slightly decurrent at the auricles, not plicate (sometimes irregularly striate in the short-celled phase), oblong-lanceolate, gradually acuminate from a lanceolate base, not secund, apex not channelled, 2.5–3.5 mm. $\times$ 0.6–0.8 mm. (1.0–3.0 mm. $\times$ 0.6–0.8 mm. in the short-celled phase; 3.0–4.8 mm. $\times$ 0.8–1.0 mm. in the aquatic phase); insertion of leaf widely to narrowly concave to circular; margin entire; costa green, extending well into the acumen, not excurrent, 40 μ in diameter at base (20–28 μ in the short-celled phase; 40–60 μ in the aquatic phase). Branch leaves similar to the stem leaves but smaller.

Cells linear, thin-walled, median leaf cells 4–6 μ $\times$ 40–60 μ (4–6 μ $\times$ 28–32 μ in the short-celled phase; 4–6 μ $\times$ 40–80 μ in the aquatic phase); alar cells inflated, large, hyaline or brown, 12–16 μ $\times$ 40–60 μ , forming distinct groups extending $\frac{1}{4}$ – $\frac{1}{2}$ the distance from the margin to the costa.

HABITAT: Ponds and pools in bogs and swamps, grassy marshes, wet meadows, and wet depressions in woods, stones and logs in old river beds, frequently growing in water. Thirty-five feet is the greatest depth at which this variety has been reported (*Coville and Applegate 1141*, from Linn County, Oregon).

ILLUSTRATIONS: Husnot, *Musc. Gall. pl.* 106, f. 3, 10; short-celled phase—*pl.* 106, f. 1, 2, 7, 9, 10; aquatic phase—*pl.* 107, f. 1; Pascher, *Süsswasser-Fl.* (2 ed.) 14: 153, f. 53 e; short-celled phase—14: 133, f. 47 f, i; (2 ed.) 14: 153, f. 53 c; aquatic phase—14: 133, f. 47 e; (2 ed.) 14: 153, f. 54 d; Mönkemeyer, *Laubm. Eur.* 756, f. 171 e; short-celled phase—f. 171 c; aquatic phase—f. 171 d.

EXSICCATI—*D. aduncus* var. *Kneiffii*: MASSACHUSETTS: N. A. M. Pl. 160 (DUKE, NY); OHIO: M. Bor. Am. Ed. 2, 1865, 466 (MICH); WISCONSIN: N. A. M. Pl. 181 (DUKE, MICH); N. A. M. Pl. 188; (DUKE, MICH, NY); YUKON: Can. Musci 361 (NY);



MAP 1. DISTRIBUTION OF DREpanocladus ADUNCUS

DREpanocladus ADUNCUS var. *capillifolius* (Warnst.) Wynne, stat. nov.

Hypnum capillifolium Warnst. *Bot. Zeit.* 35: 478. 1877.

Drepanocladus capillifolius Warnst. *Beihefte z. Bot. Centralbl.* 13: 400. 1903.

D. aduncus f. *capillifolia* Mönkem. in Pascher *Süsswasser-Fl.* 14: 135, f. 47 g. 1914.

Plants green to yellow-green, deep-brown below; stems short and erect (3–7 cm. long in the short-celled phase) or long and floating, 9–15 cm., simple to irregularly or regularly pinnately branched, branches 5–25 mm. long; apical buds of stems and branches falcate-secund.

Stem leaves clasping at the base, 0.4–0.5 mm. (0.3–0.4 mm. in the short-celled phase) distant on the stem, decurrent at the auricles, not plicate or striate (sometimes striate in the short-celled phase), falcate,

lanceolate, gradually acuminate from a long lanceolate base, 3.7–5.5 mm. $\times$ 0.6–1.0 mm. (2.0–3.0 mm. $\times$ 0.5–0.9 mm. in the short-celled phase); insertion of the leaf narrowly concave or circular, margin entire; costa strong, green or brown, 60–80 μ in diameter at base (40 μ in the short-celled phase), long excurrent.

Cells linear, thin-walled, median leaf cells 4–8 μ $\times$ 60–80 μ (4–6 μ $\times$ 20–32 μ in the short-celled phase), alar cells inflated, large, hyaline or colored, 16–20 μ $\times$ 40–80 μ , forming distinct auricles usually extending from the margin to the costa.

HABITAT: Partly or entirely submerged in pools in bogs and swamps; ponds; ditches; springs; sometimes in calcareous places.

In the original description, Warnstorf compares this plant to both *D. aduncus* and *D. fluitans* as follows: “. . . Stengel so kräftig wie flutende Formen von *Hypnum fluitans* Dill. und *aduncum* Schpr. . . . Stengelblätter . . . schwach sichelförmig gekrümmt wie bei *Hypnum fluitans* und *aduncum* . . . Im äusseren Habitus zeigt das Moos noch die meiste Aehnlichkeit mit *Hypnum fluitans* und manchen Formen des polymorphen *H. aduncum* . . .” He describes the margin as “schwach gesägt” but does not mention the transition from the stem to leaf cells, one of the best differentiating features between *D. aduncus* and *D. fluitans*. His description of the cells of the leaf fits *D. aduncus* very closely: “Zellen eng und lang, nur über dem Blattgrunde weiter und kürzer, etwa doppelt so lang wie breit . . .” In 1903 he placed *Drepanocladus capillifolius* under “*Aduncus*-Gruppe” so it is obvious that the affinities of the original plant are with *D. aduncus* rather than with *D. fluitans*.

Mönkemeyer (1914), in the first edition of Pascher's “Süßwasser-Flora” was the first to attach var. *capillifolius* to *D. aduncus*. All plants with excurrent costae, entire leaf margins, and a gradual transition from cells of the leaf to cells of the stem belong to *D. aduncus* var. *capillifolius*. Plants with excurrent costae, serrulate leaf margins, and an abrupt transition from the cells of the leaf to cells of the stem belong to the parallel variety of *D. exannulatus*, var. *Rotae*. Forms with excurrent costae do not occur in *D. fluitans*.

ILLUSTRATIONS: Husnot, Musc. Gall. pl. 107, f. 9; Pascher, Süßwasser-Fl. 14: 133, f. 47 g; (2 ed.) 14: p. 156, f. 55 b; short-celled phase—14: 133, f. 47 h; (2 ed.) 14: 155, f. 54 b; Mönkemeyer, Laubm. Eur. 759, f. 173 f; short-celled phase—f. 173 b.

EXSICCATI—*D. aduncus* var. *capillifolius*: WISCONSIN: N. A. M. Pl. Suppl. 55 (NY); MONTANA: N. A. M. Perf. 225 (BART); COLORADO: N. A. M. Pl. 445 (DUKE, BART, NY); N. A. M. Pl. 459 (MICH, NY, BART); WASHINGTON: N. A. M. Pl. 187 (BART, MICH, NY); OREGON: N. A. M. Pl. 332 (NY); QUEBEC: N. A. M. Pl. 246 (DUKE, MICH, NY); N. A. M. Pl. 246a (NY); ONTARIO: N. A. M. Pl. Suppl. 27 (NY).

DREPANOCLADUS FLUITANS (Hedw.) Warnst. Beihefte z. Bot. Centralbl. 13: 404. 1903.

Hypnum fluitans Hedw. Sp. Musc. 296. 1801; Bry. Eur. Mon.

Hypnum 33, pl. 602. 1854.

Amblystegium fluitans DeNot. Comment. Crittogam. Ital. 3(2): 290. 1867.

Hypnum Jamesii Aust. Bot. Gaz. 2: 142. 1877 (type seen).

H. fluitans var. *Jamesii* Lesq. & James, Man. 384. 1884 (type seen).

Harpidium fluitans Lange & C. Jens. Meddel. om Grønland 3(2): 321. 1887.

Autoicous. Plants light green, yellowish, chestnut-brown, or dark brown, seldom red or purple. Stems usually soft and slender, 5–30 cm. long, 0.2–0.4 mm. in diameter, simple or irregularly to pinnately branched, the cross-section showing a small central strand embedded in loose, thin-walled ground tissue surrounded by 2–3 rows of thick-walled golden or brownish cortical cells; branches 5–10 mm. long; apical buds of stems and branches falcate-secund but not circinate.

Stem leaves 0.4–0.6 mm. distant on the stem (0.2 mm. in var. *Berggreni*), slightly secund, usually much narrower than in *D. aduncus*, narrowly long-lanceolate, gradually tapering to a long, slender, flexuose point from a narrow base, 3.0–4.0 mm. $\times$ 0.5–0.6 mm. (1.2–7.0 mm. $\times$ 0.3–1.0 mm.), not striate (except in the short-celled phase) but sometimes folded and lax, not decurrent; line of insertion of the leaf straight or widely concave; transition of stem cells to leaf cells abrupt, apparent when some cortical stem cells remain attached to the base of the leaves; margin distinctly serrulate at apex or base or both; radicles sometimes arising from the apex, margin, base or costa of the leaf; costa green, seldom brownish or deeply colored, occasionally disappearing at half the length of the leaf, usually extending well into the acumen, but never excurrent (very short and forking in var. *Berggreni*), tapering, 40 μ (16–80 μ) in diameter at base, biconvex in cross-section. Branch leaves similar to the stem leaves but smaller, 2.0–3.0 mm. $\times$ 0.3–0.4 mm.

Cells long and narrow, linear-flexuose, the median 4–6 μ $\times$ 80–120 μ (40–180 μ), uniform in size throughout the leaf, the basal rarely shorter and broader, sometimes colored, a few alar cells enlarged, hyaline or brownish, never extending to the costa, poorly delimited and gradually intergrading with the cells of the lamina, 6 μ $\times$ 60 μ (6–20 μ $\times$ 40–100 μ).

Antheridial buds in axils of the leaves, numerous; perigonal bracts ovate, ecostate; antheridia numerous, 6–12, paraphyses of 8–10 cells, perichaetium 3 mm. sheathing the base of the seta; outer perichaetial leaves ovate, 2–3 mm., ecostate; inner perichaetial leaves lanceolate, abruptly piliform, not plicate, costa extending $\frac{2}{3}$ the length of the leaf.

Seta 5–10 cm. long; capsule asymmetrical, oblong to ovate, brownish-red, 2.0 mm. $\times$ 0.7–1.0 mm., slightly contracted under the mouth, plicate when dry; exothecial cells isodiametric, 40 μ in diameter, slightly mamillate; operculum short-conic, 0.4 mm. high; annulus lacking; outer peristome red-brown, inner peristome yellow, cilia paired. Spores papillose, yellow, to olive-green, 20 μ in diameter.

TYPE-LOCALITY: Europe.

HABITAT: Pools and stagnant water in bogs and swamps; sloughs, swales, river beds, seldom in calcareous places.

GENERAL DISTRIBUTION: Circumpolar. Widespread in northern Europe, Asia, and North America; Greenland; Iceland; Spitzbergen; Bear Island; Atlantic Islands (Canary Island); New Zealand; Tasmania; Kerguelen. Common in eastern North America where it extends southward to New Jersey, West Virginia, Ohio, Michigan, and Wisconsin; in western North America only in Wyoming, Colorado, Utah, Washington, Oregon, and Alberta (Map 2).

Drepanocladus exannulatus is distinguished from *D. fluitans* by its large group of alar cells which always show an abrupt transition to the cells of the lamina. Usually correlated with this characteristic in *D. exannulatus* is a broader leaf, a more rigid, pinnate growth, and a brilliant red or purple color which rarely occur in *D. fluitans*. Distinctions between *D. fluitans* and *D. aduncus* are included with *D. aduncus*.

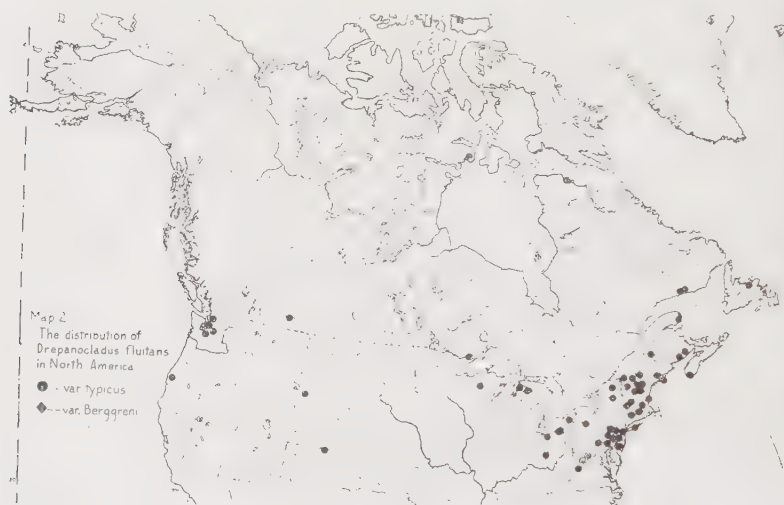
Renauld, in his treatment of section *Harpidium* in Husnot's "Muscologia Gallica" was the first to notice the characteristic abrupt transition from stem cells to leaf cells in *D. fluitans* and *D. exannulatus* (pl. 105 f. 2). Subsequent authors have not utilized the character to the extent that, in my opinion, it merits. The transition between stem and leaf cells is very easily observed because almost invariably some of the cortical cells of the stem remain attached to the base of at least a few of the leaves and the distinct line where the stem cells stop and leaf cells begin is apparent. This difference is extremely useful in distinguishing *D. fluitans* from *D. aduncus* because other criteria, such as leaf serrulation and the proportion of length to width, which are usually used in manuals, are variable and unsatisfactory.

DREPANOCLADUS FLUITANS var. **typicus** (Ren.) Wynne stat. nov.

Hypnum fluitans f. *typica* Ren. Mem. Soc. d'Emul. du Doubs Ser. V. 5 (1880): 49. 1881.

Plants green to brown; stems irregularly to regularly pinnately branched, seldom simple, falcate-secund at the apical buds.

Stem leaves 0.4–0.5 mm. (0.6–1.0 mm. in the aquatic phase; 0.2–0.4 mm. in the short-celled phase) distant on the stems, narrowly lanceolate, 3.0–4.0 mm. $\times$ 0.5–0.6 mm. (4.0–7.0 mm. $\times$ 0.4–0.6 mm. in the aquatic phase; 1.2–2.5 mm. $\times$ 0.3–1.0 mm. in the short-celled phase), not striate (except in the short-celled phase); margin distinctly serrulate at the apex or base or both; costa extending well into the apex, 40–60 μ in diameter at base (weaker in the aquatic phase).



MAP 2. DISTRIBUTION OF *DREPANOCLODUS FLUITANS*

Cells long and narrow (short and broad in the short-celled phase) the basal sometimes colored, median leaf cells 4–6 μ $\times$ 80–120 μ (4–6 μ $\times$ 20–32 μ in the short-celled phase); alar cells poorly developed, hyaline or brownish, never extending to the costa, gradually intergrading with the cells of the lamina, 6–12 μ $\times$ 50–70 μ (poorly delimited in the short-celled and aquatic phases).

ILLUSTRATIONS: Husnot, *Musc. Gall. pl.* 109, f. 1, 2, 6, 8, 9, 10; *pl.* 110, f. 2, 7, 8, 9, 14, 15, 16; aquatic phase—*pl.* 109, f. 3, 4, 5; *pl.* 110, f. 1, 3, 4, 5; Pascher, *Süsswasser-Fl.* 14: 140, f. 49 a, b, c, e; (2 ed.) 14: 162, f. 58 a, e; aquatic phase—14: 140, f. 49 d, m; (2 ed.) 14: 162, f. 58 g; p. 164, f. 59 a, e; Mönkemeyer, *Laubm. Eur.* 4: 777, f. 181 a, e, f; 779, f. 182, b, d; aquatic phase—4: 777, f. 181 g; p. 779, f. 182 a, e.

EXSICCATI—*D. fluitans* var. *typicus*: MAINE: N. A. M. Pl. 153a (NY); VERMONT: N. A. M. Pl. 277 (NY, DUKE); N. A. M. Pl. 276 (NY, DUKE, MICH, BART); MASSACHUSETTS: N. A. M. Pl. 153 (NY, DUKE); WASHINGTON: N. A. M. Pl. 242 (NY, MICH); Cascade Mts. 133 (NY, DUKE); QUEBEC: N. A. M. Pl. 341 (NY, DUKE, BART).

DREPANOCLADUS FLUITANS var. **Berggreni** (C. Jens.) Wynne stat. nov.

Harpidium fluitans subsp. *Berggreni* C. Jens. Meddel. om Grønland **3**(2): 322. 1887.

Amblystegium Berggreni C. Jens. Meddel. om Grønland **15**: 432. 1898.

Hypnum Berggreni Paris, Suppl. Index 195. 1900.

Drepanocladus Berggreni Broth. Engler und Prantl (2 ed.) **2**: 344. 1925.

Plants erect to creeping, golden to brown; stems simple or irregularly branched, apical buds falcate-secund.

Stem leaves 0.2 mm. distant on the stems, lanceolate, falcate, gradually short-acuminate, 1.2–1.6 mm. $\times$ 0.4–0.6 mm., not striate, margin distinctly serrulate at the apex or base or both; costa variable on the same plant, single and extending only half the length of the leaf, or short and forking and extending $\frac{1}{4}$ the length of the leaf, 40 μ wide at the base.

Cells long and narrow, the basal somewhat incrassate, median leaf cells 4–6 μ $\times$ 40–60 μ ; alar cells poorly developed, hyaline or brownish, never extending to the costa, gradually intergrading with the cells of the lamina, 6–12 μ $\times$ 80–100 μ .

TYPE LOCALITY: Greenland.

HABITAT: Arctic bogs and swamps, tundra.

GENERAL DISTRIBUTION: Arctic Norway, Sweden, Greenland, and Ellesmere Island.

This is an arctic variety of *D. fluitans* which differs only in the small leaves and short, weak, variable costa.

DREPANOCLADUS EXANNULATUS (Bry. Eur.) Warnst., Beihefte z. Bot. Centrabl. **13**: 405. 1903.

Hypnum exannulatum Bry. Eur. Mon. *Hypnum* **34**, pl. 603. 1854.

Amblystegium exannulatum DeNot. Epil. 142. 1869.

Hypnum fluitans var. *pinnatum* Boulay Musc. Fr. 62. 1884.

Harpidium exannulatum Lange & C. Jens. Meddel. om Grønland **3**(2): 324. 1887.

Hypnum amblyphyllum Williams Bull. N. Y. Bot. Gard. **2**: 139, pl. 24. 1901 (type seen).

Usually dioicous, occasionally autoicous. Plants more compact and rigid and less soft and flexuose than *D. fluitans*; usually red, crimson, purplish, or brownish, occasionally green or yellowish-green; stems varying in length, short and erect (5–8 cm.) in the short-celled phase or long and floating (10–30 cm.) in var. *typicus* and var. *Rotae*, simple or irregularly to pinnately branched, 0.2–0.4 mm. in diameter, showing in cross-section a small central strand embedded in loose thin-walled

ground tissue surrounded by 2-3 rows of small thick-walled cortical cells; branches 5-8 cm. (2-10 cm.) long; apical buds of stems and branches almost straight in the short celled phase, falcate-secund to circinate in var. *typicus* and var. *Rotae*.

Stem leaves 0.2-0.3 mm. distant on the stem (0.3-1.0 mm. in larger plants), not decurrent or with auricles slightly decurrent, slightly to strongly falcate, lanceolate, gradually long-acuminate from a widened base (except in the short-celled phase which is short-acuminate), 3.0-6.0 mm. $\times$ 0.6-0.8 mm. (2.0-7.0 mm. $\times$ 0.4-0.9 mm.); line of insertion of leaf straight or widely concave; transition of cortical stem cells to leaf cells abrupt; margin distinctly serrulate at apex or base or both; costa strong, usually deeply colored brown, purple, or red, reaching nearly to the leaf apex and tapering, excurrent in var. *Rotae*, 60-80 μ (20-120 μ) in diameter at base.

Cells long and narrow, median leaf cells 4-6 μ $\times$ 60-80 μ (4-8 μ $\times$ 20-120 μ in submerged plants; 4-6 μ $\times$ 20-32 μ in the short-celled phase); alar cells abruptly dilated, well developed and delimited, always extending from margin to the costa; large, inflated, hyaline and thin-walled, or colored, incrassate, and rectangular, forming either large and conspicuous auricles or a single row of large cells across the entire base.

Antheridial buds numerous; perigonal leaves ovate, briefly acuminate, ecostate, antheridia ovate-oblong, 4-6; paraphyses few, consisting of 5-6 cells. Perichaetium 3 mm. long, sheathing the base of the seta; outer perichaetial leaves ovate, abruptly short-acuminate, ecostate, or with a weak costa; inner perichaetial leaves lanceolate, abruptly and sharply acuminate, costa reaching midway.

Seta 4-7 cm. long. Capsule 2.0 mm. $\times$ 0.7 mm., not plicate, asymmetric, slightly contracted under the mouth; exothecial cells 20 μ $\times$ 40 μ toward the mouth of the capsule, 20 μ $\times$ 60 μ at base of capsule, mamilllose; operculum rostrate, 0.8 mm. high; annulus lacking; outer peristome teeth red; inner peristome segments yellow; cilia in threes. Spores olive, 20 μ in diameter.

TYPE LOCALITY: Europe

HABITAT: Lakes, stagnant pools, bogs, swamps, marshes, swampy woods, intermittent streams, alpine meadows and swamps.

GENERAL DISTRIBUTION: Circumboreal. Throughout northern Europe, Asia, and North America and southward in the mountains; Spitzbergen; Greenland; Iceland. In North America from Canada southward in the east to New Jersey, Pennsylvania, Michigan, Wisconsin, Minnesota; in the west to Colorado, Wyoming, Utah, Idaho, Alberta, British Columbia, Washington, Oregon, California, but lacking in central North America (Map 3).

Drepanocladus exannulatus and *D. fluitans* have always been confused. The differences stressed in the original descriptions are the

inflorescence and general habit of the plants, *D. exannulatus* being dioicous, robust, and deeply colored. No leaf or cellular differences were discussed. Renault in Husnot's "Muscologia Gallica" treated *D. exannulatus* as a "groupe" of *D. fluitans* and augments general distinctions of habit with some microscopic characters such as large costa and dilated alar cells which form well defined auricles. Subsequent authors have followed Renault's treatment and have added few additional distinguishing criteria.



MAP 3. DISTRIBUTION OF DREPANOCLADUS EXANNULATUS

Since European authors have called deep-purple, robust plants with large auricles *D. fluitans* in European and American material, I am convinced that microscopic leaf characters are much better criteria by means of which to separate species than characters of habit. I have used the alar cells as the final distinction between *D. exannulatus* and *D. fluitans*. Inflated, sharply delimited alar cells are usually correlated with the strong costa, robust habit, and deep color that have been associated with *D. exannulatus*. This correlation is not perfect, however, and I have considered green plants of delicate habit with inflated alar cells extending to the costa as *D. exannulatus* rather than *D. fluitans*.

European authors, including Schimper, Warnstorf, Mönkemeyer, and Roth, have emphasized the fact that *D. exannulatus* is dioicous whereas *D. fluitans* is autoicous. Renault and Dixon have indicated

that with each species the opposite type of inflorescence may occur on an occasional plant. I have found many specimens which were composed of autoicous and dioicous plants mingled in the same clump. Therefore, I believe that, when clear-cut vegetative distinctions such as the alar cells are easily seen, the character of the variable inflorescence is of less importance.

DREPANOCLODUS EXANNULATUS var. *typicus* (Dixon) Wynne, stat. nov.

Hypnum fluitans subsp. *exannulatum* group *typicum* Dixon, Handb. Brit. Mosses 520. 1904.

Plants compact, rigid, red, crimson, purplish, or brownish, green to yellow-green in some plants; stems long, 8–30 cm., (short, 5–8 cm., in the short-celled phase), simple to regularly pinnately branched, branches 5–10 cm. long; apical buds of stems and branches falcate-second to circinate; nearly straight in the short-celled phase.

Stem leaves 0.3–1.0 mm. (0.2–0.4 mm. in the short-celled phase) distant on the stem, second, or almost straight in the short-celled phase, lanceolate, gradually long-acuminate from a slightly widened base (short-acuminate from an ovate base in the short-celled phase), 3.0–6.0 mm. $\times$ 0.6–0.8 mm. (1.2–2.5 mm. $\times$ 0.3–1.0 mm. in the short-celled phase) margin serrate at base or apex or both; costa strong, deeply colored brown, purple, or red, extending into the acumens, 60–80 μ (100 μ) in diameter at the base.

Cells long and narrow, median leaf cells 4–6 μ $\times$ 60–80 μ (4–6 μ $\times$ 20–32 μ in the short-celled phase); alar cells abruptly dilated, well developed and delimited, always extending to the costa, large, thin-walled, rectangular or inflated, hyaline or colored, forming either large and conspicuous auricles or a single row of large rectangular cells across the entire base.

Since Dixon obviously intended to indicate the typical *D. exannulatus* by his use of the ambiguous category “group” I have chosen to use his treatment as the origin of var. *typicus* of *D. exannulatus*.

ILLUSTRATIONS: Husnot, *Musc. Gall. pl. 110, f. 13; pl. 111, f. 4, ?*; Mönkemeyer, *Laubm. Eur.* 4: 781, *f. 183 a, c; 782, f. 184 a; 785, f. 185 a, b, c*; short-celled phase—781, *f. 183 d*; Pascher, *Süßwasser-Fl.* (2 ed.) 14: 168, *f. 60 a, c; 169, f. 61 a, b; 170, f. 62 a*; short-celled phase—168, *f. 60 d; 169, f. 61 d*.

EXSICCATI—*D. exannulatus* var. *typicus*: VERMONT: N. A. M. Pl. 347 (NY, DUKE); N. A. M. Pl. 285 (NY, DUKE); N. A. M. Pl. 285 (NY, DUKE); N. A. M. Pl. 104 (NY, DUKE, MICH); N. A. M. Pl. 103 (NY, DUKE); NEW JERSEY: M. App. 403 (NY); WYOMING: Grand Teton Nat. Park 3765 (NY); COLORADO: N. A. M. Pl. 444 (DUKE, BART, NY); N. A. M. Pl. 461 (DUKE, MICH, BART, NY); LABRADOR: N. A. M. Pl. 408 (DUKE, BART, NY); NOVA SCOTIA: Can. Musci 854 (DUKE); Can. Musci 382 (NY); BRITISH COLUMBIA: N. A. M. Pl. 408 (DUKE); Can. Musci 367 (NY); ALASKA: Pac. Coast ¹⁸²³/₁₈₁₁ (NY); MIQUELON ISLAND: Mus. Am. Sept. 133 (NY).

DREPANOCLADUS EXANNULATUS var. ROTAE (DeNot.) Grout, Moss Flora **3**: 114. 1931.

Amblystegium Rotae DeNot. Comment. Crittogam. Ital. **2**(3): 290. 1867.

Hypnum exannulatum var. *Rotae* Pfeff. Naturf. gesells. Graubünden, Chur. Switz. 78. 1868; Neue Denksch. Allg. Schweiz. Gesells. f. ges. Naturw. **24**: 87. 1871.

Dichelyma longinerva Kindb. Bull. Torrey Club **16**: 97. 1887 (type seen).

Hypnum longinerve Kindb. in Macoun Can. Cat. **6**: 230. 1892.

Drepanocladus Rotae Warnst. Beihefte z. Bot. Centralbl. **13**: 403. 1903.

D. exannulatus f. *Rotae* Mönkem. in Pascher Süßwasser-Fl. **14**: 144. 1914.

Plants purplish, reddish, or brown; stems varying in length, 5–10 cm. and simple or irregularly branched, or 20–30 cm. and pinnately branched; branches up to 10 mm. long.

Leaves more widely spaced on stems than in var. *typicus* (0.5–1.0 mm.), long-lanceolate, 4.0–5.0 mm. $\times$ 0.5–0.7 mm. (1.2–2.5 mm. $\times$ 0.3–1.0 mm. in the short-celled phase; 3.5–7.0 mm. $\times$ 0.4–0.9 mm. in the aquatic phase), falcate; costa strong, 80–100 μ (60–120 μ) in diameter at base, long excurrent.

Cells linear-flexuose, median leaf cells 6 μ $\times$ 60–80 μ (4–6 μ $\times$ 20–32 μ in the short-celled phase); alar region well developed as in var. *typicus*, cells usually colored except in the short-celled phase.

HABITAT: Partly or entirely submerged in pools in bogs and swamps; ditches; springs; ponds; sometimes in calcareous places.

Drepanocladus exannulatus var. *Rotae* is paralleled in *D. aduncus* by var. *capillifolius*. In both cases, the excurrent costa distinguishes these varieties from all other plants in the genus. *D. exannulatus* var. *Rotae* can easily be separated from *D. aduncus* var. *capillifolius* by its serrulate margin, longer leaf cells, and the alar cells characteristic of *D. exannulatus*.

ILLUSTRATIONS: Husnot, Musc. Gall. pl. 111, f. 1; Pascher, Süßwasser-Fl. **14**: 140, f. 49 n; (2 ed.) **14**: 170, f. 62 c, d; Mönkemeyer, Laubm. Eur. **4**: 783, f. 184 c, d.

EXSICCATI—*D. exannulatus* var. *Rotae*: COLORADO: N. A. M. Pl. 439 (NY); WASHINGTON: Cascade Mts. 133 (DUKE); ALBERTA: N. A. M. Pl. Suppl. 14 (DUKE, NY, BART); BRITISH COLUMBIA: N. A. M. Pl. 159 (NY).

DREPANOCLADUS UNCINATUS (Hedw.) Warnst. Beihefte z. Bot. Centralbl. **13**: 417. 1903.

Hypnum uncinatum Hedw. Sp. Musc. 287. 1801; Bry. Eur. Mon. *Hypnum* 31, pl. 600. 1854.

Stereodon uncinatus Mitt. Journ. Linn. Soc. **8**: 43. 1865.

Amblystegium uncinatum DeNot. Comment. Crittogam. Ital. 2(3): 290. 1867.

A. aduncum L. ex Lindb. M. Scand. 33. 1879.

Harpidium uncinatum Lange & C. Jens. Meddel om Grønland 3(2): 323. 1887.

Amblystegium uncinatum var. *suetum* Sanio, K. Sv. Vet.-Akad. Handl. 23(10): 118. 1890.

Monoicous. Plants bright green, yellow-green, golden-yellow, or stramineous, seldom brownish and never red or purple; stems creeping in wide, thin mats or erect in thick tufts in var. *subjulaceus*, 1–12 cm. long, flexuose and slender or erect and stiff; often not branched or with irregular short branches when growing close and erect, or irregularly to regularly pinnately branched when prostrate; branches 3–6 mm. (1–10 mm.); apical buds of stems and branches uncinately by the falcate leaves; pseudoparaphyllia present in the axils of the branches.

Stem leaves crowded, 2–3 mm. (1–4 mm.) distant on the stems, falcate to circinate, regularly and strongly plicate both wet and dry, lanceolate with a long, subulate, serrulate acumen from a lanceolate, usually entire, base; 2.4–4 mm. (1.8–5.5 mm.) $\times$ 0.4–1.0 mm., slightly or not at all decurrent; line of insertion of the leaf straight or slightly concave; costa extending about half the length of the leaf, disappearing in the acumen, tapering, 30 μ (20–60 μ) in diameter at the base. Branch leaves similar to stem leaves but smaller, 2.0–3.0 mm. $\times$ 0.4–0.5 mm.

Cells narrowly linear flexuose, median leaf cells 4 μ $\times$ 40 μ (4–6 μ $\times$ 32–60 μ), broader at the base of the leaf; occasional leaves with slightly thickened walls; alar cells numerous, quadrate, hyaline, sometimes slightly inflated, 12 μ $\times$ 20–40 μ (8–16 μ $\times$ 12–60 μ) extending up the margin of the leaf but usually not forming distinct auricles; transition from alar cells to cells of the lamina of the leaf gradual.

Antheridial buds numerous along stems and branches; outer perigonal leaves ovate-lanceolate, ecostate; inner perigonal leaves long-acuminate from an oblong base; antheridia numerous, elongate; paraphyses long. Perichaetium elongate, 5–6 mm. sheathing the seta; perichaetial leaves very long and sheathing, erect, 3.0–8.0 mm. $\times$ 0.4–0.5 mm., strongly and regularly plicate with a long filiform acumen, not falcate, serrulate above, costa extending $\frac{1}{3}$ the length of the leaf.

Seta 2–3 cm. (4 cm.) long; capsule cylindric, arcuate, asymmetric (symmetric and erect in var. *symmetricus*), smooth, slightly contracted below the mouth when dry and empty, reddish to brownish; exothecial cells 12–20 μ $\times$ 32–38 μ (20–36 μ $\times$ 32–40 μ); operculum short conic, briefly apiculate, 3 mm. high, annulus of three rows of cells, persistent; peristome perfect, outer peristome reddish to brown; inner peristome yellow; spores olive, 12–15 μ in diameter.

TYPE LOCALITY: Europe.

larly and strongly plicate both wet and dry, lanceolate with a long, subulate, serrulate acumen, from a lanceolate, usually entire base; 2.4–4.0 mm. $\times$ 0.4–1.0 mm., slightly or not at all decurrent; costa extending about half the length of the leaf, disappearing in the acumen, tapering, 30 μ in diameter at the base.

Cells narrowly linear-flexuose, median leaf cells 4 μ $\times$ 40 μ broader at the base of the leaf with occasionally slightly thickened walls; at the basal angles numerous quadrate hyaline cells, sometimes slightly inflated, 12 μ $\times$ 20–40 μ , extending up the margin of the leaf but usually not forming distinct auricles and not sharply delimited from the cells of the lamina.

EXSICCATI—*D. uncinatus* var. *typicus*: VERMONT: N. A. M. Pl. 101 (DUKE, BART); N. A. M. Perf. 58 (DUKE, BART); Hand Lens Mosses 77 (NY); MINNESOTA: N. A. M. Pl. 223 (NY); COLORADO: N. A. M. Pl. 366 (DUKE, NY); WASHINGTON: Hand Lens Mosses 153 (DUKE); NOVA SCOTIA: Can. Musci 879 (DUKE); N. A. M. Pl. 462 (BART); YUKON: Can. Musci 363 (NY); BRITISH COLUMBIA: N. A. M. Pl. 106 (NY, DUKE); Can. Musci 657 (NY).

DREPANOCLADUS UNCINATUS var. SUBJULACEUS (Bry. Eur.) Warnst. Beihefte z. Bot. Centralbl. 13: 418. 1903.

Hypnum uncinatum var. *subjulaceum* Bry. Eur. Mon. *Hypnum* 31, pl. 600. 1854.

H. orthothecioides Lindb. Spitzb. Mossor. 540. 1866.

Harpidium uncinatum var. *orthothecioides* Lange & C. Jens., Meddel. om Grønland 3(2): 323. 1887.

Hypnum uncinatum var. *subjulaceum* f. *orthothecioides* Ren. in Husnot, Musc. Gall. 378, pl. 108, f. 10. 1894.

H. uncinatum var. *subjulaceum* f. *Holzingeri* Ren. Bot. Gaz. 30: 125. 1900.

Drepanocladus uncinatus var. *subjulaceus* f. *orthophylla* Warnst. Beihefte z. Bot. Centralbl. 13: 418. 1903.

Hypnum orthothecioides var. *suborthothecioides* Paris. Index (2 ed.) 3: 66. 1904.

Drepanocladus orthothecioides Roth, Eur. Laubm. 2: 551. 1905.

Plants golden, yellow, stramineous, or rarely yellow-green, robust, stems 4–10 cm. (2 cm.) long, unbranched, or with short, irregularly spaced branches 3–10 mm. long, erect; apical buds of stems and branches falcate-second to uncinat.

Stem leaves large, 4.4–5.5 mm. $\times$ 0.7–1.0 mm., crowded 2–3 mm. (1–4 mm.) on the stem, broadly lanceolate with a long serrulate acumen from a broad-lanceolate base, usually not serrulate at base, falcate to circinate, regularly and strongly plicate, not at all or slightly decurrent; line of insertion truncate or somewhat concave; costa extending well into the acumen, tapering, 60–80 μ in diameter at base.

Median leaf cells 4–6 μ $\times$ 50–60 μ , cells somewhat larger than in var. *typicus*, alar region as in var. *typicus*.

HABITAT: Usually on soil, logs, or rocks.

GENERAL DISTRIBUTION: Most common in western North America where it occurs in Alaska, Washington, Oregon, British Columbia, Idaho; also in Quebec and Newfoundland.

EXSICCATI—*D. uncinatus* var. *subjulaceus*: WASHINGTON: Cascade Mts. 132 (DUKE, MICH, NY); Cascade Mts. 131 (NY, MICH).



MAP 4. DISTRIBUTION OF DREPANOCLADUS UNCINATUS

DREPANOCLADUS UNCINATUS var. SYMMETRICUS (Ren. & Card.)
Grout, Check List 16, 1929.

Hypnum symmetricum Ren. & Card. Bot. Gaz. 14: 99. 1889.

Plants bright green, yellow-green, or golden-yellow to stramineous; stems creeping in wide, thin mats, 1–12 cm. long, often not branched or with irregular short branches, or regularly pinnately branched; branches 3–6 mm. long; apical buds of stems and branches uncinately.

Stem leaves crowded, 2 mm. on stems, falcate to circinate, regularly and strongly plicate both wet and dry, lanceolate with a long, subulate, serrulate acumen from a lanceolate, usually entire base; 2.8–3.9 mm. $\times$ 0.4–0.7 mm., slightly or not at all decurrent; costa extending about half the length of the leaf, disappearing in the acumen, tapering, 30 μ in diameter at the base.

Cells narrowly linear-flexuose, median leaf cells 4 μ $\times$ 40 μ , broader at the base of the leaf, with occasionally slightly thickened walls; at the basal angles numerous quadrate hyaline cells, sometimes slightly inflated, 12 μ $\times$ 20–40 μ , extending up the margin of the leaf but

usually not forming distinct auricles and not sharply delimited from the cells of the lamina.

Capsule erect, cylindric, symmetric, 1.5–2.0 mm. $\times$ 0.2–0.4 mm., smooth, slightly contracted below the mouth when dry and empty, reddish to brownish; exothecial cells $12\ \mu \times 32\text{--}36\ \mu$; peristome perfect.

HABITAT: On soil, rocks, logs, base of trees.

GENERAL DISTRIBUTION: Montana, Idaho, Washington, Oregon, California, British Columbia, Chile, Patagonia, Fuegia, Magellan region of South America, Antarctica.

The original description states that "This plant is a subspecies of *H. uncinatum* Hedw., from which it differs in the less strongly and less regularly plicate leaves, entire or very slightly denticulate, and chiefly in the narrower, erect, and quite symmetric capsules, sometimes clustered by two in the same perichaetium." The specimens which I examined, some of which were from the type localities (Oregon, *Th. Howell*; Lake Pend d'Oreille, *Leiberg*) showed no differences in plications or serrulations from *D. uncinatus* var. *typicus*.

EXSICCATI—*D. uncinatus* var. *symmetricus*: COLORADO: Mus. Am. Sept. 335 (NY, MICH); WASHINGTON: N. A. M. Pl. 207 (BART); BRITISH COLUMBIA: N. A. M. Pl. 107 (NY).

DREPANOCLADUS VERNICOSUS (Lindb.) Warnst. Beihefte z. Bot. Centrabl. 13: 402. 1903.

Hypnum vernicosum Lindb. in Hartm. Skand. Fl. (8 ed.) 342. 1861; Bry. Eur. Mon. *Hypnum* Suppl. 4, pl. 4. 1866.

Amblystegium vernicosum Lindb. M. Scand. 33. 1879.

Harpidium vernicosum C. Jens. Meddel. om Grønland 3(2): 326. 1887.

Amblystegium lycopodioides var. *vernicosum* Lindb. & Arn. K. Sv. Vet.-Akad. Handl. 23(10): 121. 1890.

Dioicous. Plants usually yellow-green, sometimes stramineous or brownish, but never red or purple; stems rigid, erect, and simple to weak, prostrate, and regularly pinnately branched, 3–20 cm. long, without a central strand, loose central tissue surrounded by a cortex of small, incrassate cells, 0.4–0.5 mm. in diameter. Branches 2–10 mm. long, in the pinnately branched forms graduated in length to make a lanceolate frond; apical buds of stems and branches always strongly uncinat.

Stem leaves 0.4–0.6 mm. distant on the stems, falcate, concave, irregularly to regularly finely plicate both wet and dry, broadly lanceolate from a short, wide, oblong base rapidly and shortly blunt acuminate, not decurrent, not auriculate, 2.0–3.0 mm. $\times$ 0.5–0.8 mm. (1.8–4.4 mm. $\times$ 0.4–1.0 mm.) long, margin entire; line of insertion of leaf truncate; costa extending $\frac{2}{3}$ the length of the leaf, disappearing

in the acumen, tapering, 40–50 μ (20–72 μ) wide at base, without a central strand. Branch leaves similar to the stem leaves but smaller, 1.0–1.3 mm. $\times$ 0.3–0.5 mm.

Cells narrowly linear-flexuose, median leaf cells 4–6 μ $\times$ 40–60 μ (8 μ $\times$ 80 μ); marginal cells at the shoulder the same size, apical cells shorter, 4–6 μ $\times$ 20 μ (8 μ $\times$ 40 μ); alar cells not differentiated at the basal angles; at the insertion 2–3 rows of hyaline or brownish, wide, oblong, hexagonal cells 8–20 μ $\times$ 12–30 μ (40 μ), with the extreme basal row always hyaline and somewhat larger than the two rows of often colored cells above.

Male plants bearing numerous lateral antheridial buds. Perigonial leaves ovate, shortly and abruptly acuminate, ecostate; antheridia 6–8, ovate to broad-lanceolate, paraphyses numerous, of 5–6 cells. Perichaetium elongate, 5 mm. sheathing the base of the seta; perichaetial leaves broadly lanceolate, smooth or very irregularly and faintly sulcate, entire, 3.0–4.0 mm. $\times$ 0.8–1.0 mm., costa extending $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf; outer perichaetial leaves broadly lanceolate, secund; inner perichaetial leaves long-lanceolate, straight.

Seta 5–7 cm. long; capsule cylindric, arcuate, asymmetric, smooth, or lightly striate at base, slightly contracted below the mouth when dry and empty, reddish to brownish; exothecial cells isodiametric, 28 μ ; operculum conic, 0.9 mm. high; annulus persistent, of three rows of cells; peristome perfect, outer peristome deep yellow, inner peristome pale, cilia 3. Spores smooth, drab, 16–20 μ in diameter.

TYPE LOCALITY: Stockholm, Sweden.

HABITAT: Bogs.

GENERAL DISTRIBUTION: Circumboreal. Northern Europe, Asia, and North America; Bear Island; Greenland. In North America common in the eastern part ranging southward to New Jersey, Michigan, Indiana; in the western part of North America only in Washington and Yukon.

Drepanocladus vernicosus differs from all other species of the genus in its stem structure and can easily be identified by examining stem sections. It is also distinct because of its plicate leaves with a short abrupt acumen and its lack of any inflated alar cells. Although it may resemble *D. revolvens* in habit, it is easily separated by its thin-walled median leaf cells, short, plicate leaves, short costa, and numerous thin-walled sub-hexagonal basal cells.

ILLUSTRATIONS: Husnot, *Musc. Gall. pl. 112*, f. 1, 2, 3, 4; Pascher, *Süßwasser-Fl.* 14: 130, f. 45 f; (2 ed.) 14: 147, f. 50 a; Mönkemeyer, *Laubm. Eur.* 771, f. 178 a.

EXSICCATI—*D. vernicosus*: CONNECTICUT: N. A. M. Pl. 391 & 391a (BART, NY); NEW YORK: M. App. 402 (NY); NEW JERSEY: M. App. 403 (NY); WASHINGTON: Cascade Mts. 134 (MICH, NY).

DREPANOCLADUS REVOLVENS (Turn.) Warnst. Beihefte z. Bot. Centralbl. **13**: 402. 1903.

Hypnum revolvens Turner, Musc. Hibern. 188. 1804; Bry. Eur. Mon. *Hypnum*, 32, pl. 601. 1854.

H. aduncum var. *revolvens* Weber & Mohr, Bot. Taschb. 361. 1807.

Hypnum intermedium Lindb. in Hartm. Skand. Fl. (9 ed.) part 2, 17. 1864.

H. Cossoni Bry. Eur. Mon. *Hypnum* Suppl. 1, 5, pl. 5. 1866.

Amblystegium revolvens DeNot. Epil. 140. 1869.

A. intermedium Lindb. M. Skand. 33. 1879.

Hypnum intermedium var. *Cossoni* Sanio, Bot. Centralbl. **2**(II Gratis-Beilage): 22. 1880.

H. revolvens subsp. *Cossoni* Ren. Rev. Bry. **8**: 79. 1881.

H. revolvens subsp. *intermedium* Ren. Rev. Bry. **8**: 79. 1881.

H. intermedium var. *revolvens* Sanio, Bot. Centralbl. **13**: 432. 1883.

Amblystegium intermedium var. *revolvens* Vent. & Bott. Atti. Soc. Crittog. Ital. **3**: 164. 1884.

Harpidium revolvens Lange & C. Jens. Meddel. om Grønland **3**(2): 322. 1887.

H. intermedium Lange & C. Jens. Meddel. om Grønland **3**(2): 325. 1887.

Hypnum revolvens f. *typica* Ren. in Husnot Musc. Gall. 391. 1894.

H. revolvens var. *intermedium* Ren. in Husnot Musc. Gall. 392. 1894.

Drepanocladus intermedius Warnst. Beihefte z. Bot. Centralbl. **13**: 402. 1903.

D. Cossoni Roth, Eur. Laubm. **2**: 548. 1905.

Monoicous, sometimes dioicous. Plants yellow-green to red at tips, red to brown, sometimes black at base, tufts often beautifully variegated and colored, glossy, sometimes with an almost metallic sheen. Stems 6–8 cm. (2–12 cm.) long, simple or irregularly, seldom pinnately, branched, appearing robust and julaceous by the imbrication of the circinate leaves; branches 2–10 mm. (15 mm.) long; apical buds of stems and branches uncinat.

Stem leaves often brilliantly colored, sometimes red and green or bright crimson, clasping the stem, crowded, 0.1–0.3 mm. distant on the stems, neither decurrent nor plicate, strongly and regularly circinate, usually forming a complete circle, concave, lanceolate, 2.0–3.0 mm. $\times$ 0.5–0.6 mm. (1.7–5.0 mm. $\times$ 0.3–1.0 mm.), with an abrupt, long, fine acumination from a widely oblong base; line of insertion of leaf truncate, not concave, margin entire or sinuate, never serrulate; costa narrow, 20–40 μ in diameter at base, extending $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf. Branch leaves similar to the stem leaves, often the same size.

Cells long and narrow, incrassate at base, uniform in size and shape

to the base, median leaf cells $4\ \mu \times 40\text{--}80\ \mu$ ($100\ \mu$); at the insertion deeply colored, with much thickened and porose walls, extending in one or two rows across the entire base, no enlarged or differentiated alar cells.

Antheridial buds ovate, on stems in the axils of the leaves, perigonal leaves long-ovate to oblong, ecostate, $1.0\ \text{mm.} \times 0.6\ \text{mm.}$; antheridia and paraphyses few; perichaetium $3\ \text{mm.}$ sheathing the base of the seta; outer perichaetial leaves ovate, ecostate, spreading with a long, abrupt acumination; inner perichaetial leaves long-lanceolate, gradually acuminate, irregularly striate, with the costa extending half the length of the leaf.

Seta $3\text{--}4\ \text{cm.}$ long, red; capsule ovate, mamilllose, not or only slightly striate when dry, asymmetric, slightly contracted under the mouth when dry and empty, $1.4\text{--}2.0\ \text{mm.} \times 0.6\text{--}1.0\ \text{mm.}$; exothecial cells $32\ \mu \times 40\ \mu$; operculum conic, $0.6\ \text{mm.}$ high; annulus of three rows of cells, persistent, peristome perfect, outer peristome yellow, inner peristome pale, cilia paired; spores yellow, $20\ \mu$ in diameter.

TYPE LOCALITY: Europe.

HABITAT: Arctic and boreal bogs and swamps.

GENERAL DISTRIBUTION. Circumboreal. Northern Europe, Asia, and North America; Spitzbergen; Iceland; Greenland. In North America from Alaska to Baffin Island, and Labrador south to Massachusetts, New York, Michigan, Iowa, Wyoming, Colorado, Alberta, and British Columbia (Map 5).

Drepanocladus revolvens is one of the most characteristic and clear-cut species in the genus. The color, the tumid stems, and the strongly uncinate tips of the stems and branches are characteristic. It is distinguished from *D. uncinatus*, the only other species with strongly circinate leaves, by its entire margin, the absence of any auricles, the lack of plications, and the characteristically abrupt, narrow acumination. The short, almost blunt, apex of *D. vernicosus* may occur in some leaves of *D. revolvens*, but, nevertheless, *D. revolvens* is distinct because it lacks any striations, has a central strand in the stem, incrassate, porose basal cells, and a characteristic red color.

ILLUSTRATIONS: HUSNOT, *Musc. Gall. pl. 112, f. 4, 5, 7-13*; PASCHER, *Süsswasser-Fl. 14: 130, f. 45 a e*; (2 ed.) **14: 149, f. 51 a**; MÖNKEMEYER, *Laubm. Eur. 773, f. 179 a, b, c*.

EXSICCATI—*D. revolvens*: OHIO: M. Bor. Am. Ed. 1, 1856, 314 (NY, MICH); Ed. 2, 1865, 464 (MICH); SASKATCHEWAN: Can. Musci 365 (NY); British Columbia: N. A. M. Pl. 97 (DUKE, NY); Can. Musci 362 (NY).

Drepanocladus intermedius has been separated from *D. revolvens* as a variety, subspecies, or a separate species on the basis of the following differences: more slender habit, smaller leaves, shorter acumination, pale yellow or green color, shorter and less deeply colored leaf cells,

and a dioicous inflorescence. All these diagnostic features are a matter of degree in their difference from *D. revolvens* and they all break down upon analysis.

Size is variable under different environmental conditions. A statistical study of leaf length shows the group of plants that I have considered as *D. revolvens* to be a unit—a single population.¹



MAP 5. DISTRIBUTION OF DREPANOCLADUS REVOLVENS

The acumination proves to be an unsatisfactory character; I have found acuminations varying in length from 0.1 to 0.8 mm. on the same plant. Color is an unsafe criterion to use as a distinction between *D. revolvens* and *D. intermedius* as there may be variation in color from light green to deep red or black in a single clone of moss depending upon the amount of exposure to sunlight. Furthermore, green color cannot be used with a short acumination as a distinguishing characteristic, for I have found no correlation between the two features. Differences in the inflorescence are not consistent, as both monoicous and dioicous plants have been found in the same tuft. I have found no justification for a sub-species or variety *intermedius* in American material and so placed the name *intermedius* in synonymy.

European specimens and published records indicate that there, also, the distinctions are not clear-cut. The few published measurements

¹ Bull. Torrey Club 71: 207-225. f. 1, 2. 1944.

of European material I have found show a complete gradation in leaf size. For instance, Renaud gives as dimensions for *H. intermedium*, 2.5–3 mm., for *H. revolvens* 3–4 mm.; and for *H. Cossoni* 3–5 mm. It is impossible to separate varieties with these measurements. Renaud further says that *H. intermedium* is very near to *H. revolvens* and is related to it by transition forms. Dixon says of *H. intermedium*, "In its best marked forms very different from *H. revolvens* but every transitional form may be found and these occur even in the same tuft" [italics mine].

Drepanocladus revolvens is a characteristic and clear-cut species; I see no need for varieties or sub-divisions within it.

DREPANOCLADUS LYCOPODIOIDES (Brid.) Warnst. Beihefte z. Bot. Centralbl. 13: 401. 1903.

Hypnum lycopodioides Brid. Sp. Musc. Suppl. 2, 227. 1812;
Bry. Eur. Mon. *Hypnum*, 45, pl. 613, 614. 1854.

Amblystegium lycopodioides DeNot. Comment, Crittogam. Ital. 2(3): 289. 1867.

Harpidium lycopodioides Lange & C. Jens. Meddel. om Grønland 3(2): 326. 1887.

Dioicous. Plants robust, growing creeping or erect, deep golden at the growing tips, deep brown below. Stems simple to fastigately branched, or the main stems subdivided into several stems of equal length, 4–30 cm. long, slender, but appearing tumid because of the densely crowded, large, concave leaves. Apical buds of stems and branches falcate-secund.

Leaves broadly lanceolate, crowded on the stems (0.1–0.2 mm.) tapering to a long acumination, 3.2–5.0 mm. $\times$ 1.0–1.4 mm. (3.0–5.5 mm. $\times$ 0.7–1.6 mm.), concave, falcate, irregularly plicate when dry, not decurrent, narrowed at the base; margin entire or faintly serrulate at the apex; line of insertion truncate to shallowly concave; costa 40–52 μ (28–60 μ) wide at the base, tapering, extending $\frac{2}{3}$ the length of the leaf, but not reaching into the acumen. Branch leaves similar to the stem leaves but smaller.

Cells long-rectangular, median leaf cells 4–6 $\mu \times$ 40–60 μ (4–6 $\mu \times$ 36–80 μ), apical and basal cells shorter; all cell walls incrassate, basal cells porose, not differentiated at the basal angles, but two rows across the entire base very incrassate, golden-yellow, and pitted.

Antheridial buds numerous on male plants; perigonial leaves ovate, abruptly acuminate, ecostate. Perichaetial leaves broadly lanceolate, falcate, sulcate, costa weak, extending $\frac{1}{4}$ – $\frac{1}{2}$ the length of the leaf.

Seta 3–5 cm. long. Capsule cylindric, slightly curved, 3–4 mm. $\times$ 0.7–1.0 mm.; operculum conic, short apiculate; annulus triseriate, peristome perfect, outer peristome deep yellow to reddish-brown; inner peristome yellow, cilia paired. Spores 20 μ in diameter.

TYPE LOCALITY: Europe.

HABITAT: Pools in bogs and swamps.

GENERAL DISTRIBUTION. Circumboreal. Arctic Europe south to the British Isles; Siberia; Greenland, Ellesmere Island.

Although *D. lycopodioides* resembles *Scorpidium scorpioides* in habit, it can be distinguished by means of its single costa. Large plants of *D. uncinatus* var. *subjulgatus* are distinct because of their thin-walled cells, serrulate apex, and regular, strong plications. Robust plants of *D. revolvens* differ from *D. lycopodioides* in their strongly and regularly circinate leaves with slender, almost filiform, acuminations.

ILLUSTRATIONS: Husnot, *Musc. Gall.*, pl. 107, f. 8; Pascher, *Süsswasser-Fl.* 14: 132, f. 46; (2 ed.) 14: 151, f. 52; Mönkemeyer, *Laubm. Eur.*, 768, f. 177a.

Drepanocladus lycopodioides is widespread, although not common, in Europe. In North America it has been collected in Greenland by Lange and C. Jensen and in the Canadian Eastern Arctic by Nicholas Polunin as follows: Hudson Bay Company Post, South Bay, Southampton Island, Aug. 22, 1936, *Polunin 2293a-1* (MICH); Port Harrison, Quebec, Aug. 6-9, 1936, *Polunin 1569a-10* (MICH). Renauld and Cardot report it for Miquelon Island in their *Flora Miquelonensis* p. 53, 1888. The description above is based on American plants supplemented with European material.

DREPANOCLADUS BADIUS (Hartm.) Roth, *Eur. Laubm.* 2: 569. 1905.

Hypnum badium Hartm. *Skand. Fl.* (5 ed.) 332. 1849.

Amblystegium badium Lindb. *M. Scand.* 33. 1879.

Calliergon badium Kindb. *Eur. and N. Amer. Bryin.* 82. 1897.

Dioicous. Plants in small tufts, rigid, prostrate to erect. Stems green, golden or copper-colored at growing tips, reddish-brown or black below, 4-8 cm. long, simple or with a few scattered branches.

Stem leaves clasping the stem at intervals of 0.1-0.3 mm., not decurrent, ovate to lanceolate, abruptly or gradually short acuminate, not twisted at the apex, not striate nor plicate, concave, some leaves slightly falcate, others on the same plant straight; line of insertion truncate or shallowly concave; margin entire and plane; costa 20-40 μ wide at the base, extending $\frac{1}{2}$ - $\frac{3}{4}$ the length of the leaf. Branch leaves similar to the stem leaves but smaller, 0.5 mm. $\times$ 1.0 mm.

Cells linear-flexuose, incrassate, reddish, and porose, secondary cell walls of two basal cells 6-8 μ thick, 3-5 pits between adjacent cells, median leaf cells 4 μ $\times$ 40 μ (4-6 μ $\times$ 20-50 μ), apical and basal cells shorter; alar cells small, 12-20 μ $\times$ 16-28 μ , thick-walled (10-12 μ), in small, poorly defined groups extending half the distance

from the margin to the costa or in a single row extending across the entire base.

Antheridial buds numerous, lateral; perigonial leaves ovate, abruptly acuminate, ecostate, 0.6 mm. $\times$ 0.4 mm.; perichaetium sheathing the base of the seta, perichaetial leaves long-lanceolate, slightly sulcate.

Seta 3-5 cm. long, capsule cernuate, oval, turgid, not plicate, 2 mm. $\times$ 1.2 mm., exothecial cells $12\ \mu \times 40\ \mu$, smooth; operculum short conic; peristome perfect, outer peristome reddish-brown, inner peristome yellow, cilia paired.

TYPE LOCALITY: Northern Scandinavia.

HABITAT: Often forming large masses of vegetation in the arctic swamps and tundra.

GENERAL DISTRIBUTION. Arctic Scandinavia; Spitzbergen, Arctic Asia; Greenland; Yukon Territory; Baffin Island. In the literature, Labrador (*Allen*) is also cited for North America, but I have not seen the material, nor can I find the original reference.

Drepanocladus badius is distinct from all other species of *Drepanocladus* in its short, ovate, straight or slightly falcate leaves with incrassate, porose cell walls. *D. lycopodioides*, the only other species with thickened porose cell walls, is a much larger, more robust plant.

ILLUSTRATIONS: Brotherus, *Laubm. Fennoskand.* 481, f. 92; Mönkemeyer, *Laubm. Eur.* 775, f. 180 a, b.

SPECIMENS FROM NORTH AMERICA EXAMINED: Amardjak Bay, Baffin Island, Aug. 2, 1926. *J. Dewey Soper 894, Canadian Nat. Herb.* 892 (MICH).

DREPANOCLADUS BREVIFOLIUS (Lindb.) Warnst. *Beihefte z. Bot. Centralbl.* 13: 416. 1903.

Hypnum brevifolium Lindb. *Ofversigtkong. Vetes.-Akad. Förhandl.* 23: 541. 1866.

Hypnum lycopodioides var. *brevifolium* Berggr. *K. Sv. Vet.-Akad. Handl.* 13(7): 83. 1874.

Amblystegium latifolium Lindb. & Arn., *K. Sv. Vet.-Akad. Handl.* 23(10): 120. 1891.

Drepanocladus latifolius Warnst. *Beihefte z. Bot. Centralbl.* 13: 415. 1903.

Drepanocladus latinervis Warnst. *Beihefte z. Bot. Centralbl.* 13: 416. 1903.

Plants golden at the growing tips, brown to black below, dull. Stems prostrate or erect, simple or irregularly branched, 3-8 cm. long, 0.2 mm. in diameter, in cross-section showing a small central strand, loose ground tissue, and a cortex composed of narrow, thick-walled cells; apical buds of stems and branches falcate-secund.

Leaves clasping, 0.2-0.3 mm. distant on the stems, not decurrent, ovate to broadly lanceolate, gradually short acuminate, 0.6-2.4 mm.

× 0.6–1.0 mm., falcate, abruptly narrowed at the base; line of insertion shallowly concave or truncate; margin faintly serrulate or sinuolate at the base; costa variable, single, and extending half the length of the leaf, or short and double, 40 μ in diameter at the base.

Cells linear-rectangular, porose, slightly incrassate, or thin-walled, but with all cell walls of the same thickness, median leaf cells 6–8 μ × 40–60 μ , shorter at the apex and base, not inflated at the basal angles, but some leaves with a row of slightly larger cells across the insertion.

Sporophyte unknown.

TYPE LOCALITY: Spitzbergen,

HABITAT: Arctic swamps and bogs.

GENERAL DISTRIBUTION: Circumpolar in the northern hemisphere; Spitzbergen, Bear Island; Siberia; Greenland; North Devon Island; Ellesmere Island; Baffin Island; Alaska.

Drepanocladus brevifolius is the only species of *Drepanocladus* in which the cell walls are uniform in thickness and porose throughout the leaf and the costa is variable. In *D. badius* all the cell walls are porose but noticeably more incrassate at the base, and the costa is always single. In *D. fluitans* var. *Berggreni*, the only other species with a variable costa, the cells are not porose and only slightly incrassate.

SPECIMENS FROM NORTH AMERICA EXAMINED: GREENLAND: Fort Conger, 1902, *R. E. Peary* 3 (NY); ALASKA: Barter Island, Arctic Coast, summer 1918, *J. Hadley* 60c (NY).

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DESCRIPTION OF PLATES¹

PLATE 1. DREPANOCLADUS ADUNCUS

Fig. 1, Stem leaves of var. *typicus*. Fig. 2, Apex of stem leaf of var. *typicus*. Fig. 3, 4, Branch leaves of var. *typicus*. Fig. 5, Stem leaves of var. *typicus* (short-celled phase). Fig. 6, Apex of stem leaf of var. *typicus* (short-celled phase). Fig. 7, Branch leaf of var. *typicus* (short-celled phase). Fig. 8, Stem leaf of var. *typicus* (aquatic phase). Fig. 9, Branch leaf of var. *typicus* (aquatic phase). Fig. 10, Alar region of var. *typicus*. Fig. 11, Perichaetial leaf. Fig. 12, Perigonal leaf. Fig. 13, Cross-section of leaf.

PLATE 2. DREPANOCLADUS ADUNCUS

Fig. 1, Stem leaf of var. *capillifolius*. Fig. 2, Apex of excurrent costa of stem leaf of var. *capillifolius*. Fig. 3, Stem leaf of var. *capillifolius* (short-celled phase). Fig. 4, Stem leaf of var. *Kneiffii*. Fig. 5, Apex of stem leaf of var. *Kneiffii*. Fig. 6, Branch leaf of var. *Kneiffii*. Fig. 7, Stem leaf of var. *Kneiffii* (short-celled phase). Fig. 8, Apex of stem leaf of var. *Kneiffii* (short-celled phase). Fig. 9, Branch leaf of var. *Kneiffii* (short-celled phase). Fig. 10, Alar region of var. *Kneiffii* (short-celled phase). Fig. 11, Stem leaf of var.

¹ NOTE: In these plates, all leaves are × 30 and all cells are × 160, except Plate 1, fig. 11 (× 20); Plate 3, fig. 3 (× 20); Plate 6, figs. 4–5 (× 20); and Plate 9, figs. A1–A2 (× 25).

Kneiffii (aquatic phase). Fig. 12, Alar region of var. *Kneiffii*. Fig. 13, Portion of cross-section of stem.

PLATE 3. DREPANOCLADUS FLUITANS

Fig. 1, Stem leaves of var. *typicus*. Fig. 2, Apex of stem leaf of var. *typicus* showing radicles. Fig. 3, Stem leaves of var. *typicus* (aquatic phase). Fig. 4, Branch leaf of var. *typicus* (aquatic phase). Fig. 5, Stem leaf of var. *typicus* (short-celled phase). Fig. 6, Branch leaf of var. *typicus* (short-celled phase). Fig. 7, Cross-section of leaf. Fig. 8, Alar region. Fig. 9, Portion of cross section of stem. Fig. 10, Leaf apex.

PLATE 4. DREPANOCLADUS EXANNULATUS

Fig. 1, Stem leaf of var. *typicus*. Fig. 2, Branch leaf of var. *typicus*. Fig. 3, Stem leaf of var. *typicus*. Fig. 4, Branch leaf of var. *typicus*. Fig. 5, Stem leaf of var. *typicus* (short-celled phase). Fig. 6, Branch leaf of var. *typicus* (short-celled phase). Fig. 7, Perigonal leaf. Fig. 8, Cross-section of leaf. Fig. 9, Perichaetial leaf. Fig. 10, Alar region of var. *typicus*. Fig. 11, Apex of var. *typicus*. Fig. 12, Apex of var. *typicus* (short-celled phase).

PLATE 5. DREPANOCLADUS EXANNULATUS

Fig. 1, Stem leaves of var. *Rotae*. Fig. 2, Branch leaf of var. *Rotae*. Fig. 3, Stem leaf of var. *Rotae* (short-celled phase). Fig. 4, Stem leaves of var. *typicus* (aquatic phase). Fig. 5, Excurrent costa at apex of leaf of var. *Rotae*. Fig. 6, Excurrent costa at apex of leaf of var. *Rotae* (short-celled phase). Fig. 7, Alar region of var. *Rotae*. Fig. 8, Portion of cross-section of stem.

PLATE 6. DREPANOCLADUS UNCINATUS

Fig. 1, Stem leaves of var. *typicus*. Fig. 2, Branch leaves of var. *typicus*. Fig. 3, Stem leaf of var. *subjulaceus*. Fig. 4, Inner perichaetial leaf. Fig. 5, Outer perichaetial leaf. Fig. 6, Perigonal leaf. Fig. 7, Alar region of var. *typicus*. Fig. 8, Apex of stem leaf of var. *typicus*. Fig. 9, Cross-section of leaf. Fig. 9¹, Pseudoparaphyllium. Fig. 10, Portion of cross-section of stem.

PLATE 7. DREPANOCLADUS VERNICOSUS

Fig. 1, Stem leaves. Fig. 2, Branch leaves. Fig. 3, Outer perichaetial leaf. Fig. 4, Inner perichaetial leaf. Fig. 5, Perigonal leaf. Fig. 6, Alar region. Fig. 7, Cross-section of leaf. Fig. 8, Portion of cross-section of stem.

PLATE 8. DREPANOCLADUS REVOLVENS

Fig. 1, Stem leaves. Fig. 2, Branch leaves. Fig. 3, Perichaetial leaf. Fig. 4, Perigonal leaf. Fig. 5, Portion of cross-section of stem. Fig. 6, Cross-section of leaf. Fig. 7, Alar region.

PLATE 9. DREPANOCLADUS LYCOPODIODES AND D. BADIUS

D. LYCOPODIODES

Fig. A1 Stem leaf. Fig. A2, Branch leaf. Fig. A3, Alar region. Fig. A4, Portion of cross-section of stem.

D. BADIUS

Fig. B1, Stem leaves. Fig. B2, Alar region. Fig. B3, Apex of stem leaf.

PLATE 10. DREPANOCLADUS BREVIFOLIUS AND D. FLUITANS

D. BREVIFOLIUS

Fig. A1, Stem leaves. Fig. A2, Branch leaf. Fig. A3, Alar region of stem leaf. Fig. A4, Apex of stem leaf.

D. FLUITANS

Fig. B1, Inner perichaetial leaf. Fig. B2, Outer perichaetial leaf. Fig. B3, Perigonal leaf. Fig. B4, Stem leaves of var. *Berggreni*. Fig. B5, Branch leaf of var. *Berggreni*. Fig. B6, Apex of stem leaf of var. *Berggreni*. Fig. B7, Alar region of stem leaf of var. *Berggreni*.

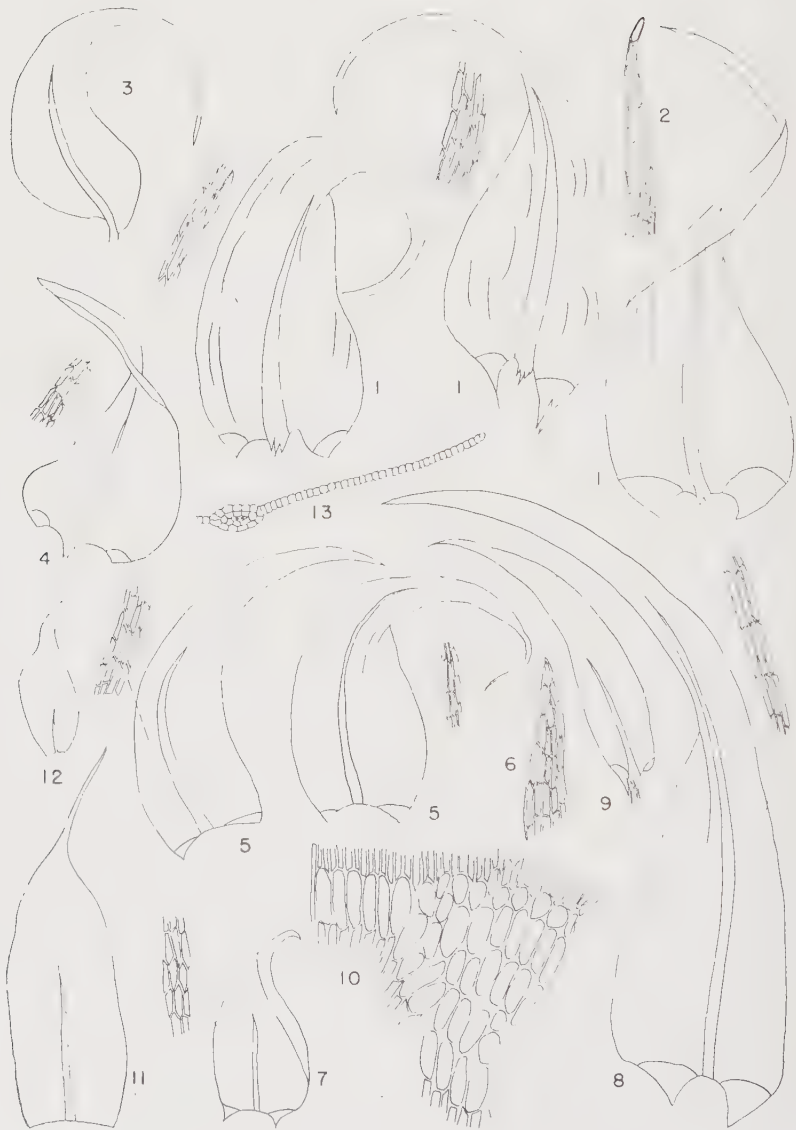


PLATE 1. DREPANOCLADUS ADUNCUS



PLATE 2. DREPANOCLADUS ADUNCUS

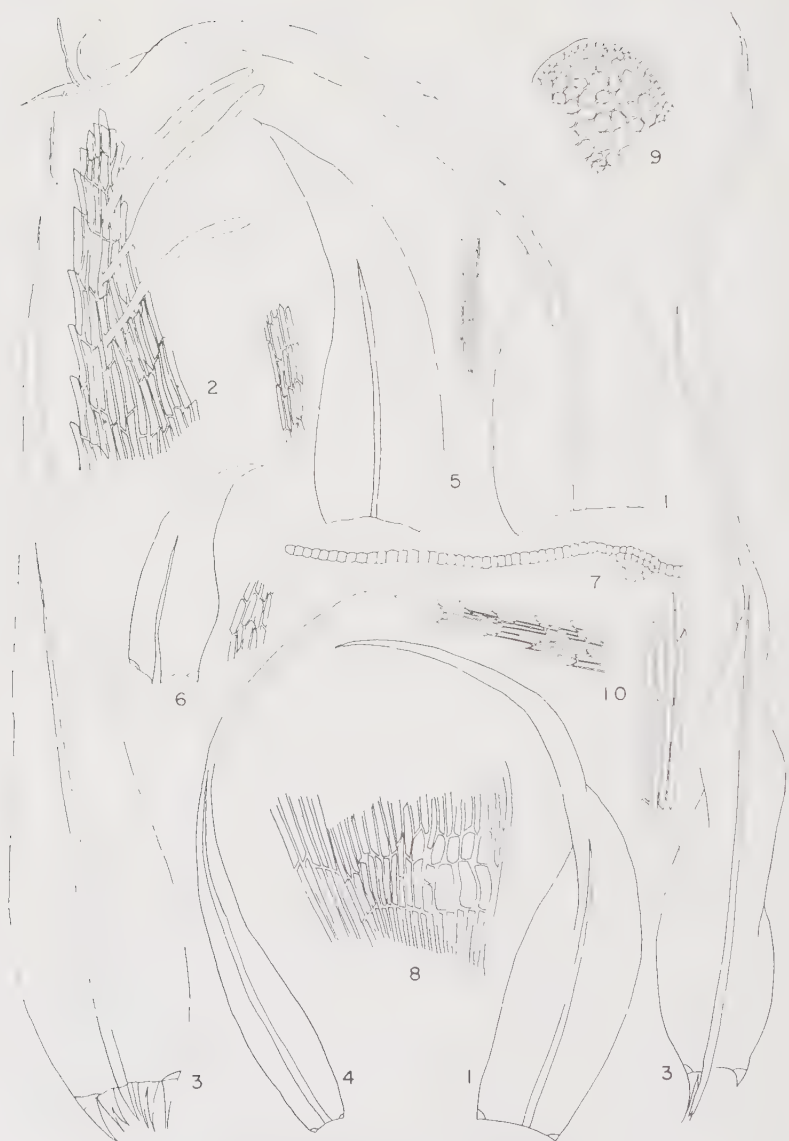


PLATE 3. DREPANOCLODUS FLUITANS



PLATE 4. DREPANOCLADUS EXANNULATUS

PLATE 5. *DREPANOCLODUS EXANNULATUS*

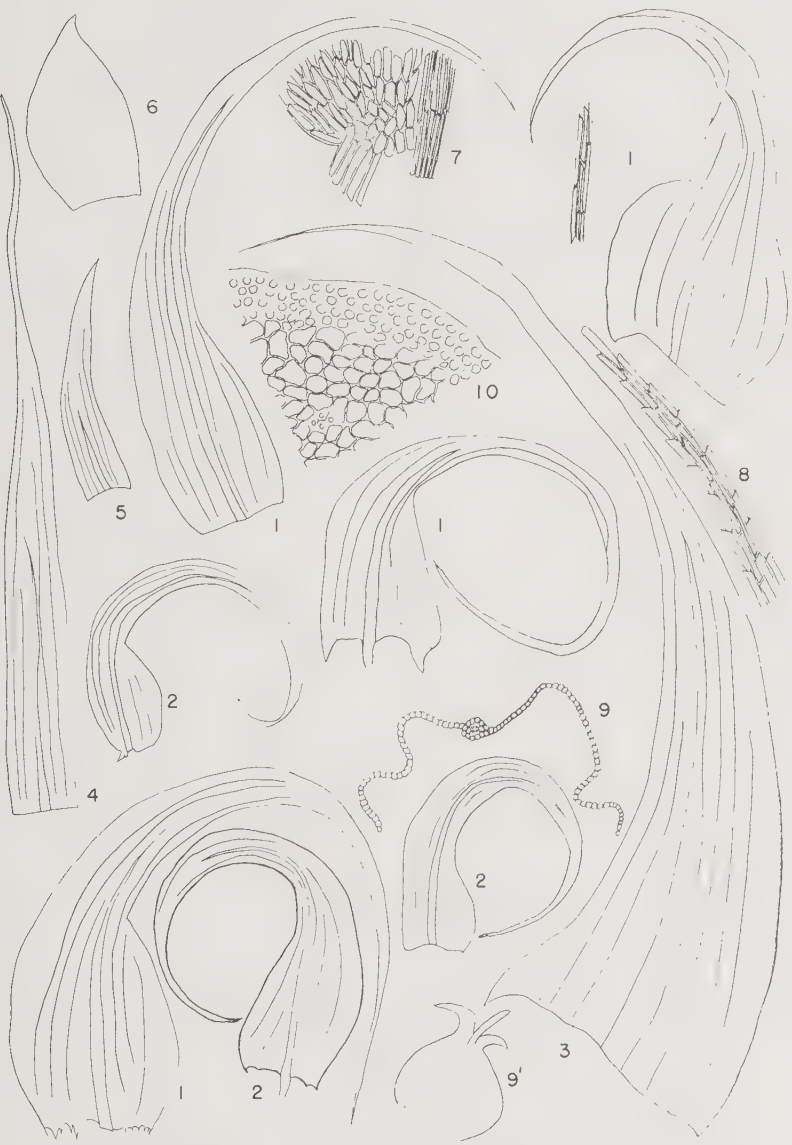
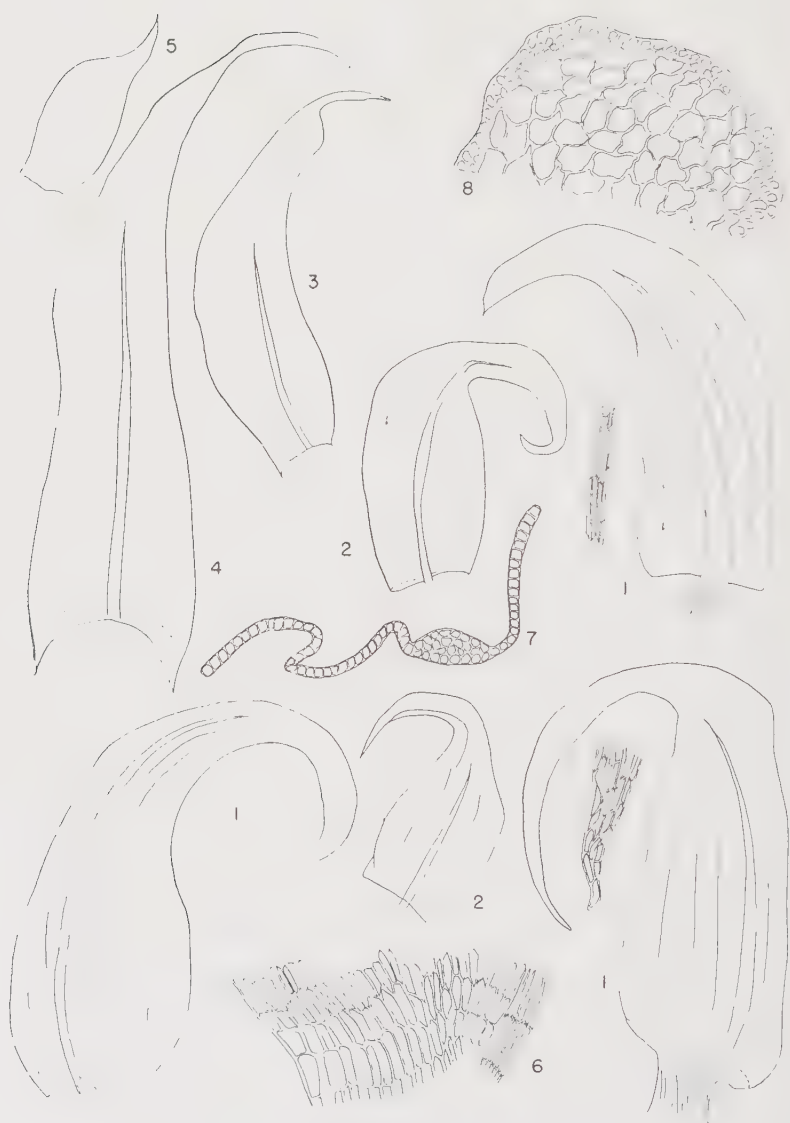


PLATE 6. DREPANOCLADUS UNCINATUS

PLATE 7. *DREpanocladus vernicosus*

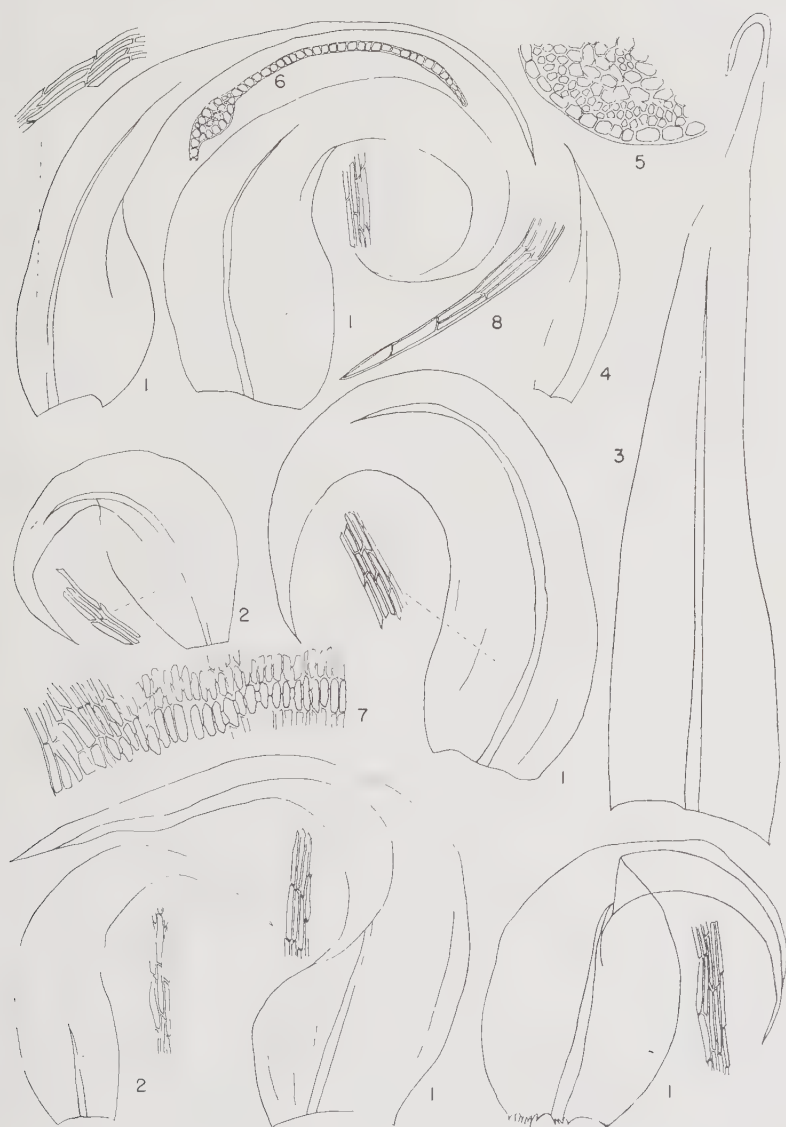


PLATE 8. DREPANOCLADUS REVOLVENS

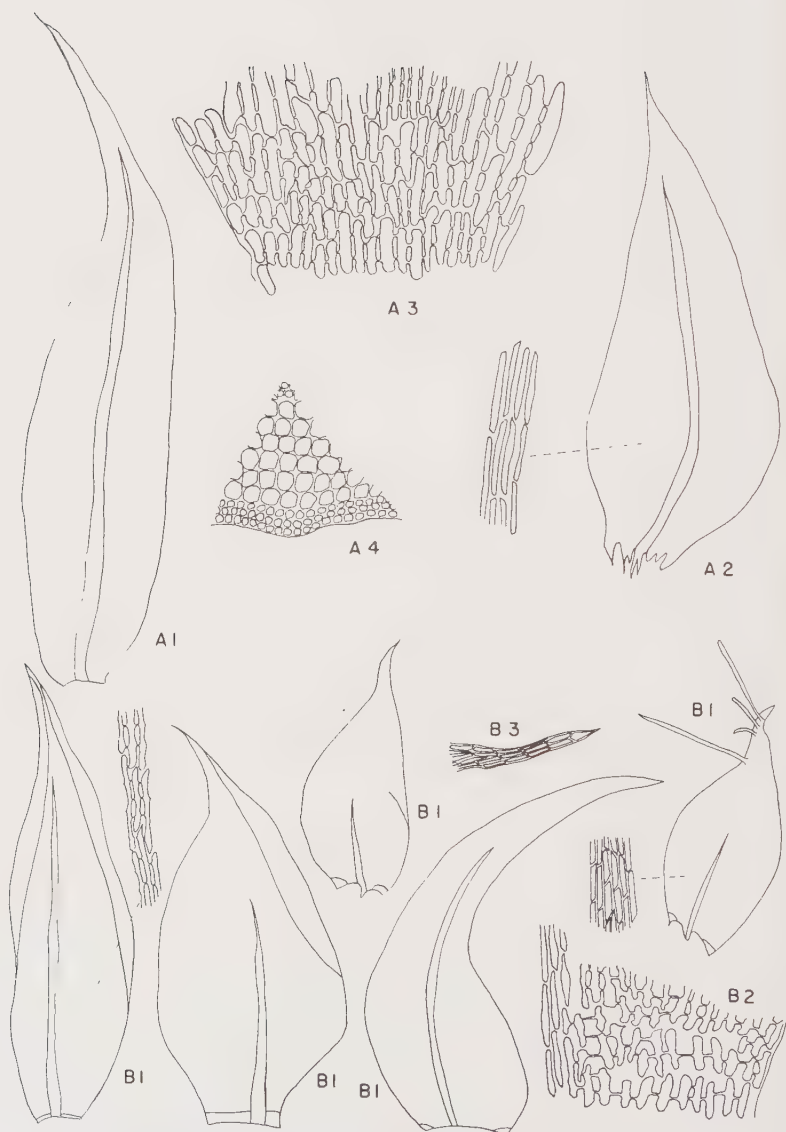


PLATE 9. DREPANOCLADUS LYCOPODIODES AND D. BADIUS

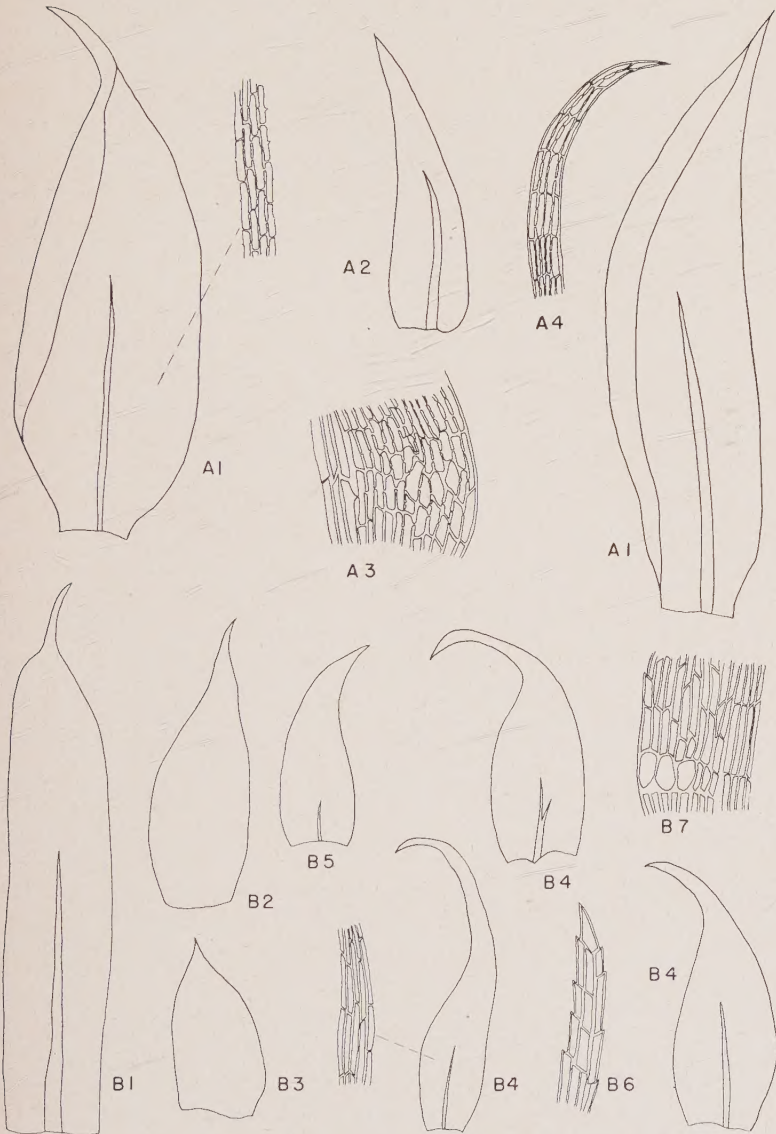


PLATE 10. DREPANOCLADUS BREVIFOLIUS AND D. FLUITANS

